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Variation in and Distribution of the Unisexual Lizard, *Cnemidophorus tesselatus*

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INTRODUCTION

The discovery that some populations of the lizard *Lacerta siccicola* (family Lacertidae) in Armenia reproduce parthenogenetically (Darevsky, 1958) was followed by the announcement that six species of the genus *Cnemidophorus* (family Teiidae) native to the United States and Mexico are all-female or virtually so (Maslin, 1962). Although parthenogenesis remains to be demonstrated experimentally in the American species, it is almost certain that this is the mode of reproduction. My purpose is to describe the individual and geographic variation of one of these species, *Cnemidophorus tesselatus*, and to compare the variation with that seen in bisexual species. Throughout this paper I use the terms "parthenogenetic," "unisexual," and "all-female" interchangeably, aware that parthenogenesis has yet to be demonstrated unequivocably and that, rarely, male lizards do occur.

The virtual absence of male lizards leads to the assumption that *Cnemidophorus tesselatus* is parthenogenetic. Maslin (1962, p. 212) examined 223 specimens of this species and found only one male among them. Tinkle (1959) found only females among 65 specimens. I examined the gonads of an additional 200 lizards without finding any males. Thus, only one

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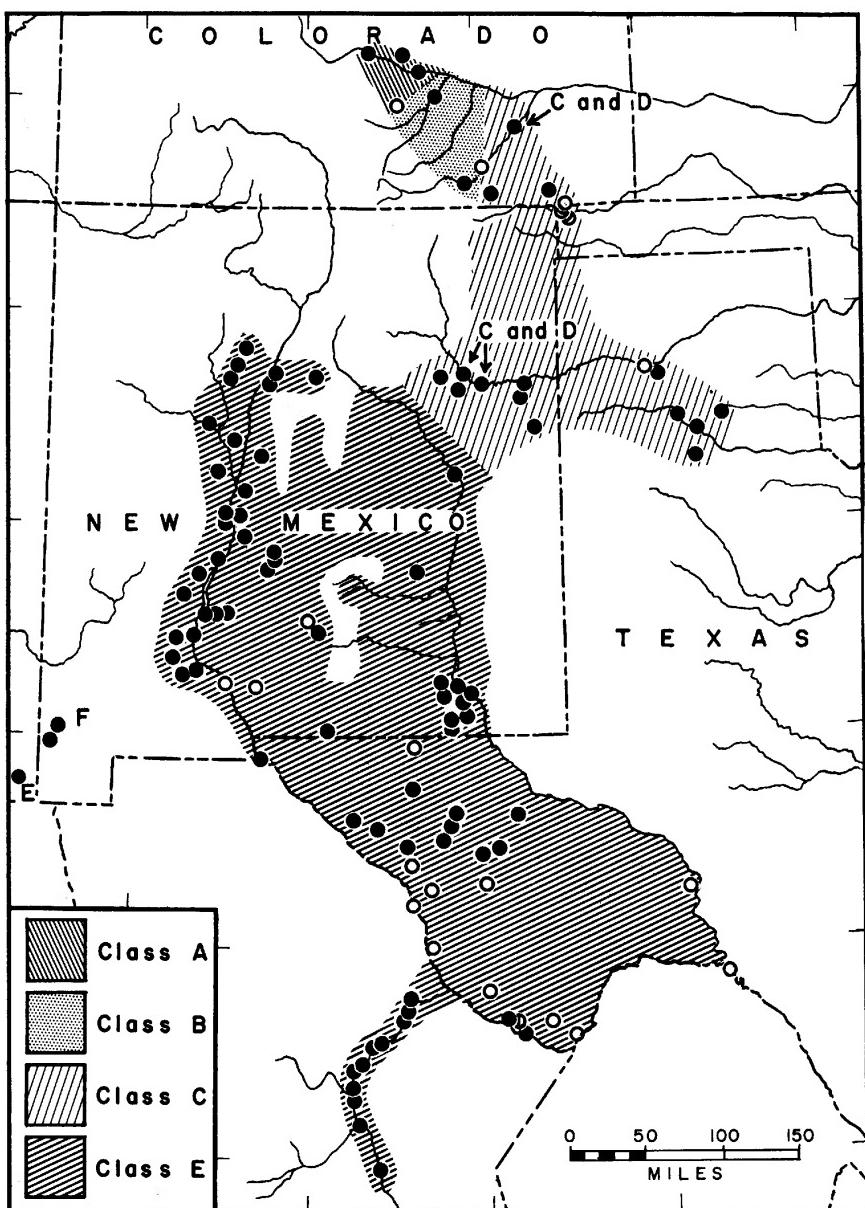


FIG. 1. Distribution of *Cnemidophorus tesselatus*. Spots indicate localities for specimens examined; circles mark literature records. Shading patterns show inferred distributions of pattern types.

male has been found among 488 specimens from all parts of the range of the species. The other investigators and I examined lizards collected in various habitats throughout their daily and seasonal periods of activity. Males would have been encountered, therefore, were they normally present in the populations sampled.

Cnemidophorus tesselatus is found throughout much of New Mexico and also occurs in southeastern Colorado, extreme western Oklahoma, western Texas, northern Chihuahua, and extreme southeastern Arizona (fig. 1). I have examined 545 specimens representing most of the range of the species. My studies were largely limited to preserved specimens, for I have had field experience with the species only in restricted areas in southwestern and central New Mexico.

Recent studies of variation in the genus *Cnemidophorus* (e.g., Lowe and Zweifel, 1952; Zweifel, 1959; Duellman and Wellman, 1960; Duellman and Zweifel, 1962) emphasize particular aspects of morphology that are most diagnostic of specific and subspecific differentiation. In this study I have concentrated on four variables in color pattern and scutellation that received closest attention in earlier work.

VARIATION IN COLOR PATTERN

Geographic and individual variation, ontogenetic change, and sexual dimorphism all influence the color patterns seen in *Cnemidophorus* and are in large part responsible for a chaotic nomenclature that only now is beginning to be clarified. Only the influence of sexual dimorphism is lacking in *C. tesselatus*.

Hatchlings of most species of *Cnemidophorus* have a body pattern of narrow light stripes on a dark ground color, in some instances with light spots in the dark fields. Some species retain the juvenile pattern essentially unchanged throughout life, but ontogenetic changes occur in the majority. Change may be so extensive that the adult bears no similarity to its offspring. There is a wide range in the patterns of adult lizards, even among races of a single species. Moreover, in polytypic species the subspecies may differ more from one another than they do from populations of other species.

Descriptions of the basic striped pattern of the body and its subsequent ontogenetic modification in *C. tesselatus* follow. There are three pairs of primary light stripes: (1) the paravertebrals arise at the parietal scales; (2) the dorsolaterals arise at the posterior corner of the eye; and (3) the laterals pass through the ear. There may be seven stripes, including the vertebral, or eight, in which case there is a pair of vertebrals. Less often there are lower lateral stripes, raising the total to 10. The dark fields between the

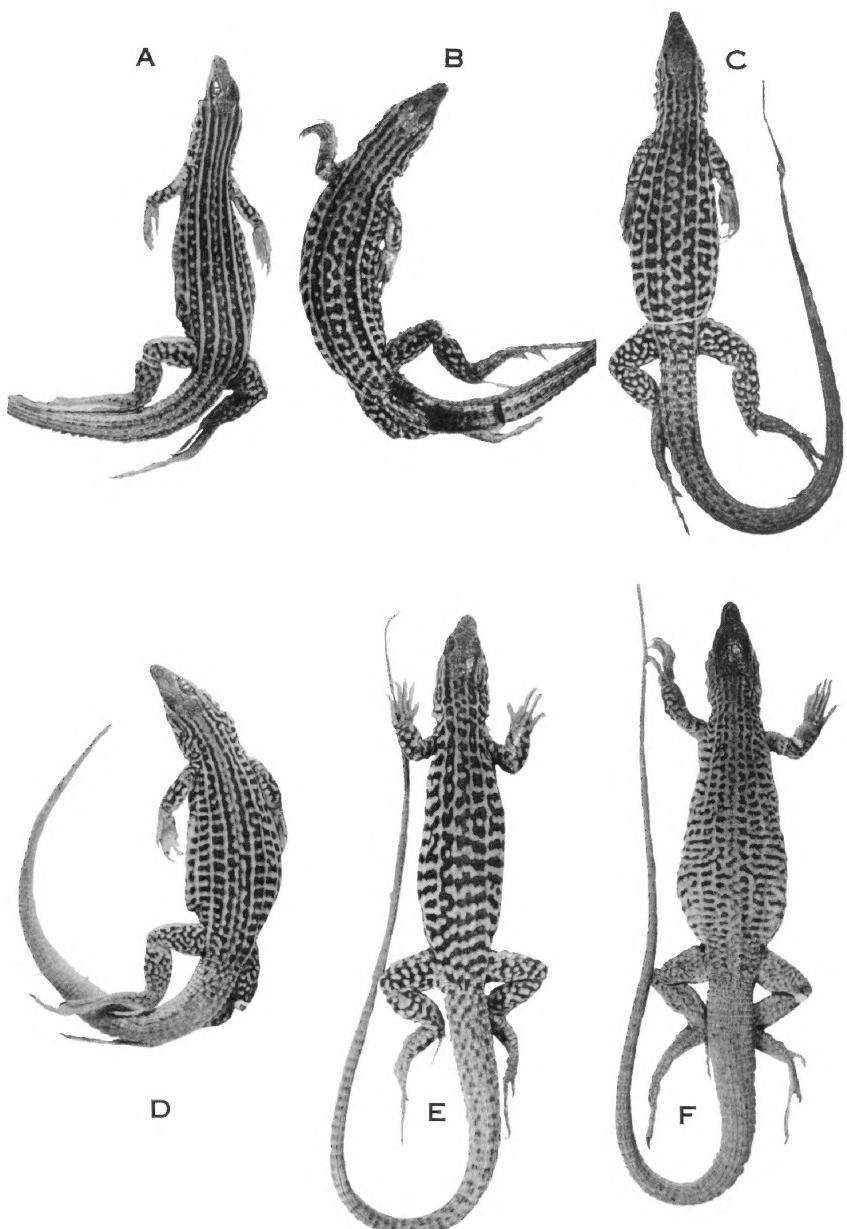


FIG. 2. Specimens exemplifying six pattern classes of *Cnemidophorus tesselatus*. Letters correspond to designations of pattern classes: A, U.C.M. No. 10366, vicinity of Pueblo, Pueblo County, Colorado; B, U.C.M. No. 16972, 25 miles southeast of Pueblo, Pueblo County, Colorado; C, J.W.W. No. 797, Conchas Lake, San Miguel county, New Mexico; D, U.C.M. No. 14830, 1 mile south of Higbee, Otero County, Colorado; E, A.M.N.H. No. 84833, vicinity of San Marcial, Socorro County, New Mexico; F, A.M.N.H. No. 80682, Antelope Pass, Peloncillo Mountains, Hidalgo County, New Mexico. One-half natural size.

stripes are: (1) the vertebral, between the paravertebral stripes; (2) the dorsolateral, between paravertebral and dorsolateral stripes; (3) the lateral, between dorsolateral and lateral stripes; and (4) the lower lateral, below the lateral stripe. Modifications in the basic pattern result mainly in two ways: (1) when light spots appear and spread in the dark fields and (2) when segments of the dark fields spread and fuse vertically, disrupting the light stripes.

PATTERN CLASS A: I refer 20 specimens from the immediate vicinity of Pueblo, Pueblo County, Colorado, two from near Stone City, Pueblo County, and one from Cañon City, Fremont County, Colorado (fig. 1), to this pattern class.

The slight degree of pattern metamorphosis attained by adult lizards (fig. 2A) is diagnostic of Class A. Hatchlings have six distinct light stripes and only faint light spotting in the lateral field. There is a seventh (vertebral) stripe on the nape, but it is represented on the trunk only by a series of spots. Most adult and subadult lizards differ from hatchlings only in having more abundant and more distinct light spots. The lower lateral fields are broken into series of dark rectangles in the largest specimens (85–87 mm. S–V) from Pueblo, and the lateral fields of one individual are similarly disrupted. The largest specimen in the series, 96 mm. S–V, is from Stone City and has the lower lateral and lateral fields quite broken up by expansion of the light spots. In all specimens the six primary lines are distinct and unbroken and the dorsolateral and vertebral fields show light spots on otherwise unbroken dark fields.

PATTERN CLASS B: This class is represented by 26 lizards from 23 to 25 miles southeast of Pueblo, Pueblo County, Colorado, and one specimen from Trinchera Canyon, 30 miles east-northeast of Trinidad, Las Animas County, Colorado (fig. 1).

Metamorphosis of pattern characteristically goes further in these lizards than in those of Class A. Three hatchlings resemble those of Class A in having six distinct primary lines and light spotting in the lateral field, but the paravertebral lines are farther apart and there is a series of wavy spots or a true vertebral line. Additional light spots appear with growth and, particularly in the lower lateral and lateral fields, expand vertically, touching the light lines. This vertical expansion fragments the lower lateral and lateral fields into a series of dark rectangles (fig. 2B). As a rule the dorsolateral field remains a continuous dark field, with light spots that do not expand. Irregular fusion of the vertebral line or spots with the paravertebral stripes generally breaks up the vertebral field.

A typical adult lizard of Class B has six distinct light stripes, the lateral and lower lateral fields broken into dark rectangles, light spots in the dark

dorsolateral fields, and an irregularly broken vertebral field. Rarely, some dark rectangles of the lateral and lower lateral fields may fuse across the lateral line, breaking the continuity of that line.

PATTERN CLASS C: Lizards of this class occur over a wide area, from Otero County in southeastern Colorado to the Panhandle region of Texas and San Miguel and Quay counties in northeastern New Mexico (fig. 1).

Metamorphosis of pattern is more complete than in lizards of Class B. Hatchlings have the usual six primary lines, but a wavy vertebral line more frequently is present, and field spotting is more prominent. Metamorphosis proceeds in the same fashion: the light field spots spread vertically and break up the dark fields (fig. 2C). The dorsolateral field, which in adult Class-B lizards normally retains a spotted appearance, is also disrupted. Although disrupted, it usually does not change into a series of relatively regular rectangles as do the lower fields but is irregularly broken or may even be transformed into a dark undulatory band.

Adult lizards typically have uninterrupted lateral and dorsolateral light lines. Rarely the lateral line is broken by fusion of dark rectangles in the lateral and lower lateral fields. In many individuals the paravertebral stripes are disrupted just anterior to the rump by irregular fusions of dark areas in the vertebral and dorsolateral fields (fig. 2C). Some large lizards, presumably those that had a strong stripe as hatchlings, retain a fairly distinct though wavy vertebral stripe.

PATTERN CLASS D: Lizards of this pattern class occur in the vicinity of Higbee, Otero County, Colorado, and in San Miguel County, New Mexico (fig. 1). In both regions lizards of Class C also occur.

The most obvious distinction between classes C and D is that the vertebral line (or series of spots) is doubled and relatively straight in Class D (fig. 2D) but single and sinuous in Class C. In addition, some lizards of Class D develop supernumerary longitudinal light lines subdividing the dark rectangles of the lateral and lower lateral fields.

Hatchlings of the Colorado population (I have seen only adults from New Mexico) have paired vertebral lines, or a series of paired spots, and the usual six primary lines. In addition, a lower lateral line is indicated at least faintly in all 23 specimens. Field spotting is prominent, and in most instances the spots are as distinct and as light as the stripes. Even in hatchlings the spots tend to spread. A unique feature of these lizards is that the spots not only spread vertically but also to some extent longitudinally, in the shape of a +. Longitudinal spreading of the light spots creates a multistriped effect in the young lizards.

As the lizard grows, the vertical spread of the light spots breaks up

the dark fields just as in other classes. Individuals with a minimum amount of longitudinal spread of light spots (fig. 2D) have a terminal pattern much like that of Class C, but the paired vertebral lines or their remnants are distinguishable and the pattern in general is more regular than that in Class C, especially in the dorsolateral dark field. Also, the dark rectangles of the lower lateral field are broken by the lower lateral line. This line, though never so prominent as one of the primary lines, is much more distinct than in Class-C lizards in which it rarely is present even in poorly developed form. In specimens (most frequent in the Colorado population) in which the longitudinal fusion of light field spots is well developed, most of the dark rectangles of both the lower lateral and lateral fields are divided horizontally so that the number of dark markings in these fields is almost doubled. Dark rectangles that are not divided may appear pinched, indicating some lateral expansion of the light field spots.

PATTERN CLASS E: Lizards with this pattern occupy the largest area within the range of the species, from the northern Rio Grande Valley in Sandoval County, New Mexico, to Chihuahua, including west Texas and eastern New Mexico southward from De Baca County. An apparently isolated population is found in southeastern Arizona (fig. 1).

In occasional adult individuals of Class C some dark rectangles of the lateral fields fuse with their neighbors in the lower lateral fields, breaking the continuity of the lateral stripe. In Class-E populations such fusion is usual, rather than a rare occurrence. The presence in large adult individuals of at least some degree of such fusion is diagnostic of Class E (fig. 2E).

Hatchlings possess six distinct light stripes on a dark brown or virtually black ground color. The vertebral stripe is undulatory and irregular. Many individuals have a series of short dashes in the vertebral field rather than a continuous line. Light spots are restricted to or most prominent in the posterior parts of the lateral dark fields. The dorsolateral fields typically are unspotted.

As the lizard grows, the light spots in the lateral fields become more distinct, and spots appear in the dorsolateral fields. The spots expand vertically, meeting the light lines and fragmenting the fields into dark rectangles, more regularly rectangular in the lateral field than in the dorsolateral field. The sequence is similar in the vertebral field, though if a strong vertebral line is present in the hatchling this line may persist so that relatively little fragmentation of the field occurs. At this stage the pattern is essentially that of Class C.

In the next phase of pattern development, vertical fusion of the dark rectangles produces vertical bars on the sides of the body. There is indi-

vidual and geographic variation in the amount of fusion in adult lizards, but typically the lateral stripe is broken in several places. In some populations fusion is restricted largely to the lower lateral and lateral fields: the dorsolateral and paravertebral light stripes remain more or less intact, and the upper lateral and vertebral dark fields are irregularly broken up or merely lightly spotted. At the other extreme (fig. 2E), the dark lateral bars extend well up on the sides and, in the lumbar region, may meet across the dorsal midline.

Dr. F. R. Gehlbach has kindly furnished notes on the color in life of a Class-E lizard from Bat Cave Draw, Eddy County, New Mexico: enlarged scales of head olive-brown; paravertebral and dorsolateral stripes yellowish or ocher-yellow; lateral stripes light yellow or yellowish white, becoming white in the axillary region; dorsal dark markings brownish black; forelimbs off-white dorsally, hind limbs ocher-yellow; tail brownish yellow at the base, becoming khaki-brown toward tip; ventral surfaces pearl-white, except yellowish white on tail, chin, and throat, with faint orange pigment.

Although the two extremes of development of Class E are quite distinct, ontogenetic variation, individual variation, lack of adequately large samples from many regions, and the necessarily subjective mode of treatment prohibit a detailed statement of geographic variation. In one region, however, populations of adjacent areas are unquestionably different. Samples from the Rio Grande Valley of New Mexico in northern Dona Ana, Luna, Sierra, and southern Socorro counties show extensive cross barring. At the other extreme are a large number of specimens from within an 8-mile radius of Socorro, Socorro County, New Mexico, and others collected 10 to 22 miles south-southwest of Bingham at the eastern edge of the Jornada del Muerto in Socorro County, about 35 to 40 miles southeast of Socorro. In these samples almost half of the adult lizards have the lateral light stripe uninterrupted by vertical spreading of the dark bars, and hence could be referred to Class C. Three lizards from the western side of Mockingbird Gap, no more than 2 or 3 miles from the southernmost of the localities on the Jornada del Muerto, contrast markedly in having well-developed lateral bars. To the west along the Rio Grande lizards of the well-barred subclass range at least as far north as San Marcial, about 22 miles south of the localities in the vicinity of Socorro. The only two specimens from Arizona (fig. 1) have the bars well developed.

There are indications of similar geographic variation in other parts of the range of Class E, though nowhere is it so clear-cut as in the Rio Grande Valley. No geographic trends are apparent; variation appears to be random. For example, lizards from the northern Rio Grande Valley in San-

doval County are more like those of Sierra County than like those of the geographically intermediate Socorro region. The large sample from along the Río Conchos in Chihuahua includes no lizards with lateral bars confluent across the back, though all adults have the lateral stripe interrupted. Four lizards from $\frac{1}{2}$ mile west of Fort Sumner, De Baca County, comprise the northernmost sample of Class E in eastern New Mexico. This is approximately 50 miles from the closest localities for lizards of Class C.

PATTERN CLASS F: This pattern class is known only from Hidalgo County in southwestern New Mexico: one specimen is from an isolated volcanic hill in Animas Valley 5 miles north of Animas, and the remaining 22 are from Antelope Pass in the Peloncillo Mountains, 7 to 10 miles west of Animas. These localities are about 90 miles from the closest locality to the east for *tesselatus* (Class E) in northeastern Luna County (fig. 1), but the isolated population of Class E in Cochise County, Arizona, is only 34 miles southwest of Antelope Pass.

Two specimens of near-hatchling size (42 and 49 mm. S-V) have a more highly metamorphosed pattern than does any other *tesselatus* of comparable size. The paired vertebral, paravertebral, and dorsolateral stripes are discontinuous even at this small body size. The lateral stripe is represented by an ill-defined line on the posterior part of the trunk. The dark fields mostly are broken into small dark rectangles. Commonly the rectangles below the dorsolateral stripe fuse vertically, resulting in the absence of a clearly defined lateral stripe. Some fusion is present even between the more dorsal fields, accounting for the discontinuous nature of the remaining light stripes. Thus, the juvenile is a faintly striped lizard with numerous small dark spots in the middorsal region and narrow vertical bars on the sides of the body.

The adult lizards (fig. 2F) closely resemble the juveniles. The light stripes, indistinct in juveniles, are even less well defined in adults. Additional fusion of dark field spots takes place, but the vertical bars thus formed are so narrow and frequently so sinuous that the strongly barred aspect of some Class-E lizards never develops. The terminal adult pattern may appear dark-spotted or reticulate, but usually combines these two patterns.

In life, lizards of Class F are predominantly brown dorsally. I recorded that one adult individual had an orange tint prominent posteriorly, whereas another adult had a slightly green cast to the brown. The under surfaces are immaculate white to grayish white. A faint iridescent pinkish tinge may be present.

SUMMARY OF VARIATION IN COLOR PATTERN: Color patterns of *Cnemidophorus tessellatus* may be classified in six categories. Adults of each

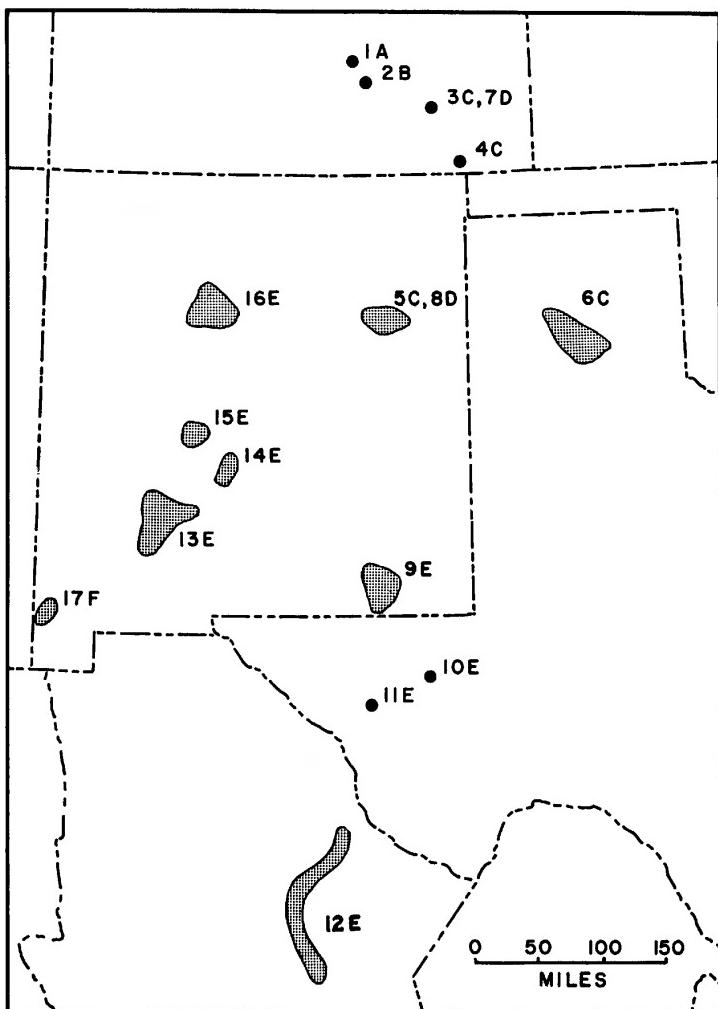


FIG. 3. Localities from which specimens used in population comparisons were drawn. Number is sample number. Letter indicates pattern class: 1A, vicinity of Pueblo, Pueblo County, Colorado; 2B, 23–25 miles southeast of Pueblo; 3C, vicinity of Higbee, Otero County, Colorado; 4C, vicinity of Carrizo Mountain, Las Animas and Baca counties, Colorado; 5C, San Miguel County, New Mexico; 6C, Armstrong, Potter, and Randall counties, Texas; 7D, vicinity of Higbee, Otero County, New Mexico; 8D, San Miguel County, New Mexico; 9E, Eddy County, New Mexico; 10E, Weinacht's Draw, Reeves County, Texas; 11E, 20 miles east of Van Horn, Culberson County, Texas; 12E, Río Conchos, Chihuahua; 13E, Sierra County, New Mexico; 14E, east side of Jornada del Muerto, Socorro County, New Mexico; 15E, vicinity of Socorro, Socorro County, New Mexico; 16E, Sandoval County, New Mexico; 17F, Hidalgo County, New Mexico.

progressively "higher" class attain a greater degree of pattern metamorphosis than do those of the class immediately below. There also is a correlation of juvenile and adult patterns, for young lizards of a "high" class have a somewhat metamorphosed pattern at hatching. As a rule, only one pattern class occurs in one locality, but lizards of classes C and D are sympatric at the only two places where Class D is found. Each class is not necessarily a homogeneous unit. Additional subunits may be detected, particularly in classes C and E, when enough specimens become available to permit detailed comparisons of local populations.

VARIATION IN SCUTELLATION

For this analysis I employed 17 samples from 15 regions, shown in figure 3. Where two pattern classes occur in one region these are treated as separate samples.

GRANULES AROUND MIDBODY: The number of dorsal granules (GAB) was counted at midbody. This character is relatively stable within local populations of *Cnemidophorus* and proves to be the best single character for the differentiation of species. In *511 tessellatus* the range is 75 to 112 GAB; data are summarized in table 1 and figure 3, and statistical comparisons are given in table 2.

The Class-A sample from Pueblo, Colorado, at the northern edge of the range, has the lowest GAB average, so this population, which is one of the most distinctive in pattern, is also well distinguished in this aspect of scutellation. Class-B lizards also have a relatively low GAB average, but it is significantly higher than that of Class A (table 3, $P << 0.001$).

Among the four Class-C samples, three (3C, 5C, and 6C) are much alike, but the one from the vicinity of Carrizo Mountain (4C) has an average notably higher than that of the others. The difference between this Class-C population and the other three contrasts with the virtual identity of samples 3C, 5C, and 6C with the Class-B sample (table 2, fig. 4).

The two areas in which Class D has been found are about 170 miles apart. Samples 7D and 8D differ significantly ($P << 0.001$) in the mean number of granules around the midbody. Comparisons of these samples with sympatric populations of Class C are made in another section.

The eight samples of classes A through D exhibit a relatively wide range in average GAB values, 14.8 scales, but seven average fewer than 92 GAB. Class E differs from these in that despite the broad geographic area from which the eight samples were drawn, the mean is consistently high, 92 GAB or higher, and the range of sample means is small, 5.8 scales. Among lizards not included in the samples treated statistically

TABLE I
VARIATION IN SCUTELLATION IN SEVENTEEN SAMPLES OF *Cnemidophorus tesselatus*
(See figure 3 for localities of samples.)

Sample	Granules around Midbody			Mean \pm σ_m	N	Mean \pm σ_m	Femoral Pores	V%	N	I	Circumorbital Type		
	Mean	Range	V%				Range				IV	III	II
1A	79.8 \pm 0.6	76-85	3.19	19	38.9 \pm 0.3	36-41	3.52	19	100% (19) ^a	—	—	—	—
2B	86.1 \pm 0.8	79-94	3.95	26	39.5 \pm 0.3	37-42	3.95	26	100% (26)	—	—	—	—
3C	86.1 \pm 1.3	82-92	3.88	7	39.5 \pm 0.5	38-42	3.57	8	33% (3)	—	67% (6)	—	—
4C	94.6 \pm 0.5	90-101	2.61	25	44.7 \pm 0.3	41-47	3.31	26	—	8% (2)	92% (23)	—	—
5C	88.7 \pm 1.1	82-97	5.46	21	41.0 \pm 0.5	38-47	5.00	21	14% (3)	14% (3)	71% (15)	—	—
6C	86.6 \pm 0.9	81-91	3.98	14	40.8 \pm 0.9	37-44	3.98	15	25% (3)	8% (1)	67% (8)	—	—
7D	91.6 \pm 0.6	86-96	3.22	24	40.1 \pm 0.3	37-43	4.18	27	63% (19)	7% (2)	30% (9)	—	—
8D	84.9 \pm 1.1	81-91	3.57	7	38.9 \pm 0.7	36-41	5.04	7	—	—	100% (7)	—	—
9E	92.7 \pm 0.4	88-96	2.00	22	41.8 \pm 0.3	39-44	3.40	22	—	23% (5)	77% (17)	—	—
10E	97.4 \pm 0.8	92-101	3.23	17	42.9 \pm 0.5	38-47	4.85	17	—	—	100% (17)	—	—
11E	97.2 \pm 0.5	93-103	2.87	33	41.3 \pm 0.2	38-44	3.25	33	—	—	100% (34)	—	—
12E	98.5 \pm 0.5	92-106	3.59	57	43.0 \pm 0.2	40-47	3.96	55	—	10% (6)	90% (54)	—	—
13E	97.5 \pm 0.7	89-110	3.79	31	44.6 \pm 0.3	40-48	3.65	36	14% (5)	5% (2)	81% (30)	—	—
14E	93.3 \pm 0.8	86-98	3.93	24	42.4 \pm 0.3	40-45	3.38	23	—	4% (1)	88% (21)	8% (2)	—
15E	95.5 \pm 0.5	89-105	3.34	42	44.0 \pm 0.2	41-48	3.43	42	—	2% (1)	95% (42)	2% (1)	—
16E	97.6 \pm 0.8	92-105	4.32	27	42.6 \pm 0.3	39-45	3.57	27	4% (1)	4% (1)	63% (17)	30% (8)	—
17F	97.5 \pm 1.0	93-112	4.60	22	42.5 \pm 0.4	39-47	4.10	23	56% (13)	35% (8)	9% (2)	—	—

^aThe number of specimens is given in parentheses.

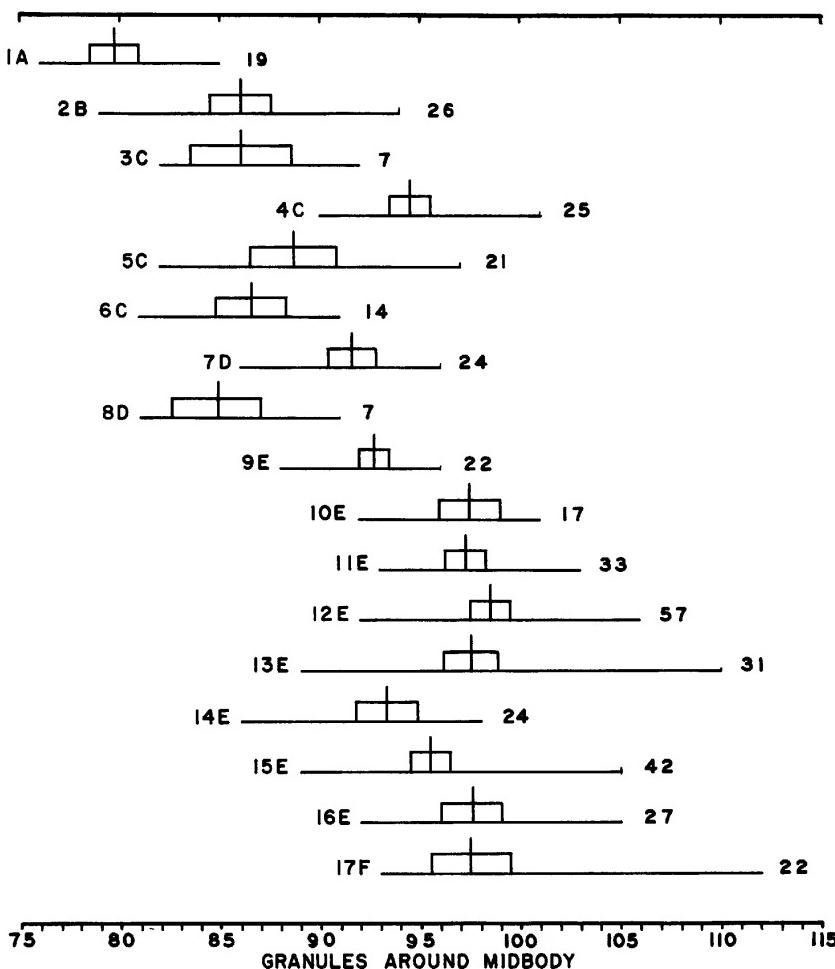


FIG. 4. Variation in numbers of granules around midbody in 17 samples of *Cnemidophorus tesselatus*. Horizontal line indicates range, vertical line mean, rectangles enclose two standard errors on each side of mean. Sample number (see fig. 3) on left and number of specimens on right.

there is only one series, that from the vicinity of Corrado Mountain in Otero County, New Mexico, with a lower mean—91.6 ($N = 10$). Most other individual specimens or short series show typically high counts, though the two specimens from the isolated population in southeastern Cochise County, Arizona, have only 88 and 91 GAB. There is a greater difference between samples 3C and 4C, from only 50 miles apart, than between any two adequate (10 or more specimens) samples of Class E

TABLE 2
COMPARISON OF MEAN VALUES OF SCALE COUNTS AMONG SEVENTEEN POPULATIONS OF
Cnemidophorus tesselatus BY MEANS OF TWO-SIDED T TESTS

Samples Compared ^a	Granules Around Midbody	Femoral Pores		
	Value of T	Probability	Value of T	Probability
1A and 2B	6.307	<<0.001	1.281	0.2
2B and 3C	0.036	0.9	0.065	>0.9
2B and 7D	5.478	<<0.001	1.437	0.2
3C and 7D	4.178	<<0.001	0.918	0.4
3C and 4C	7.575	<<0.001	8.810	<<0.001
3C and 5C	1.277	0.2	1.895	<0.1, >0.05
7D and 4C	3.946	<0.001	10.550	<<0.001
7D and 8D	5.276	<<0.001	1.511	0.1
7D and 5C	3.000	<0.01, >0.001	1.674	0.1
4C and 5C	5.395	<<0.001	7.231	<<0.001
5C and 6C	1.353	<0.2, >0.1	0.300	0.8
5C and 9E	3.637	<0.001	1.527	0.1
5C and 8D	1.945	<0.1, >0.05	2.417	0.02
8D and 9E	8.328	<<0.001	4.304	<0.001
9E and 10E	5.777	<<0.001	1.922	0.05
10E and 11E	0.126	0.9	3.371	<0.001
11E and 12E	1.739	<0.1, >0.05	4.877	<<0.001
12E and 13E	1.576	0.1	4.573	<<0.001
13E and 17F	0.236	0.8	4.682	<0.001
13E and 14E	3.882	<0.001	5.417	<0.001
13E and 15E	2.050	0.05	1.745	<0.1, >0.05
14E and 15E	2.669	0.01	4.246	<0.001
15E and 16E	2.292	0.02	3.705	<0.001
16E and 5C	6.815	<<0.001	3.105	<0.001

^a See table 1 for other statistical data and figure 3 for localities.

no matter how remote their geographic origins.

Class F resembles Class E in granule count, having a mean identical to that of the closest adequate sample of Class E, 13E.

FEMORAL PORES: The number of scales bearing femoral pores (total of both legs) varies individually and geographically in *Cnemidophorus*. Species, subspecies, and local populations may differ in the average number of pores, but commonly there is broad overlap in ranges.

The variation in number of femoral pores is summarized in tables 1 and 2 and in figure 5. Most samples from the northeastern group of populations (pattern classes A through D) have low means, with differences between the means that are not statistically significant. The conspicuous exception is sample 4C from the vicinity of Carrizo Mountain, Las An-

TABLE 3
NUMBERS OF GRANULES AROUND MIDBODY AND OF FEMORAL PORES IN SYMPATRIC SAMPLES OF *Cnemidophorus tesselatus*

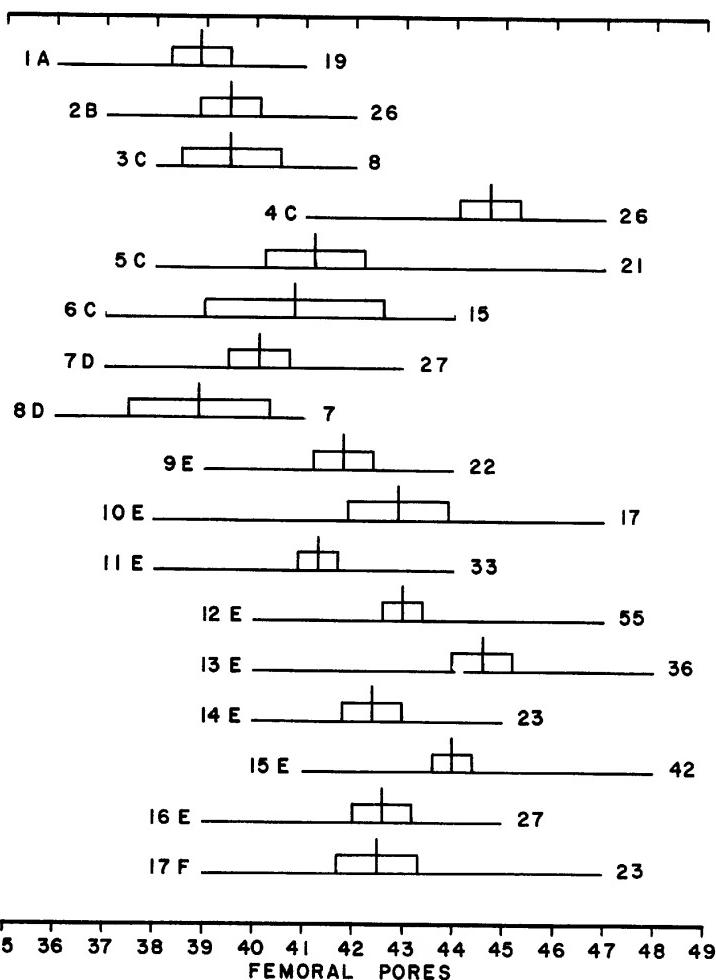


FIG. 5. Variation in numbers of femoral pores in 17 samples of *Cnemidophorus tessellatus*. See figure 4 for method of presentation.

mas and Baca counties, Colorado, which has the highest mean of any sample of *tessellatus* and differs significantly from all other samples from the northeastern part of the range.

A relatively high average number of femoral pores is the rule in classes E and F. Although in most cases the difference between the means of geographically adjacent populations is statistically significant ($P < 0.001$), no geographic trend is evident. Populations widely separated geographically may be more similar than those close together.

CIRCUMORBITAL SCALES: The circumorbitals are small scales interposed between the supraoculars and the medially located frontal and frontoparietal shields (fig. 6). There may be a complete arc of circumorbitals wholly separating the second and third supraoculars from the frontal and frontoparietal, or the circumorbital row may be incomplete, with one or more of the supraoculars in partial or complete contact with the median head scales. For the purpose of comparing individuals and pop-

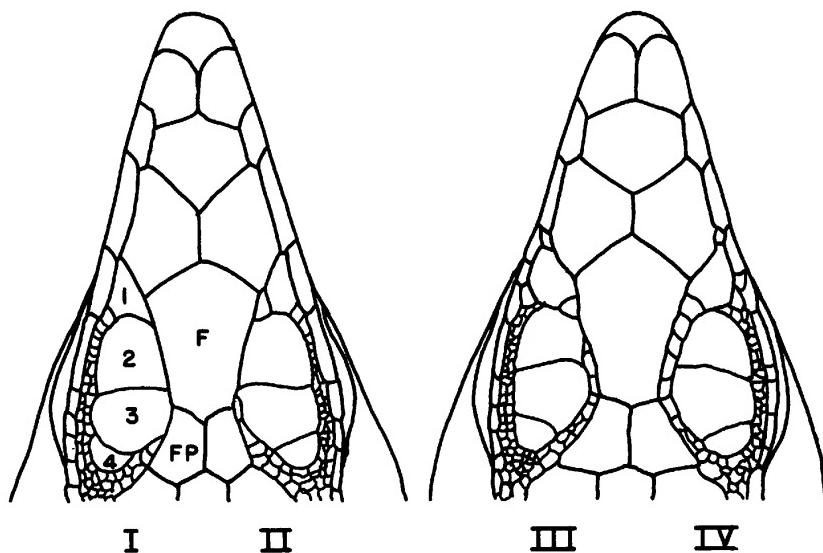


FIG. 6. Classification of circumorbital scales, the small scales intruding between supraoculars (1, 2, 3, and 4), and frontal (F) and frontoparietal (FP): I, supraocular 3 in contact with FP; II, supraocular 3 separated from FP but touching F; III, supraocular 3 separated from both FP and F, supraocular 2 touching F; IV, supraoculars 2 and 3 wholly separated from F and FP.

ulations, I have established arbitrary classes that are illustrated and defined in figure 6. The scales on the two sides of the head may be asymmetrical, or a row of circumorbitals may be discontinuous. In such cases I assigned the lizard to the lower of the two possible classes. I considered assigning fractional values, but rejected this refinement because the increased complexity of calculation and assignment to class was not warranted by the relatively small number of individuals causing the difficulty.

The usual condition in *Cnemidophorus* is a relatively short row of circumorbitals, corresponding to class I or II, though at least three species, *C. perplexus*, *C. calidipes*, and *C. parvisocius*, normally exhibit complete or

nearly complete rows, classes III and IV. The variation observed in *C. tesselatus* is summarized in table 1.

Lizards of pattern classes A and B uniformly have circumorbital scales of type I. Within Class C there is more variability, though the majority of lizards in all four samples fall in type III. One of two samples of Class D has a majority of type I, whereas type III predominates in the other. All four circumorbital types are represented in Class E, but in all samples type III dominates. Class F reverses the trend in showing a predominance of types I and II.

SUMMARY OF GEOGRAPHIC VARIATION IN SCUTELLATION: Populations from the northeastern part of the range (pattern classes A through D) tend to differ in all three characters from those occupying the southern and western part of the range. The principal exception to this statement is sample 4C from southeastern Colorado, for lizards of this sample are more like the southern lizards than they are like those from the northeastern part of the range, including other samples of Class C.

Lizards of the southern and western part of the range (classes E and F) have on the average more granules around midbody, more femoral poles, more circumorbital scales and less interpopulation variation than those in the northeastern region. The temptation to account for the meristic differences as a direct climatic effect meets with two main difficulties: (1) in the midst of the northeastern region there is the peculiar population 4C, with high ("southern") scale counts; (2) populations existing at the same latitude (but perhaps at different altitudes) in northern New Mexico, Sandoval County (16E) and San Miguel County (5C, 8D), are, respectively, clearly "southern" and "northeastern."

CORRELATION OF VARIATION IN PATTERN AND SCUTELLATION

Lizards of pattern Class E inhabit most of the range of *C. tesselatus*. Among populations of this class the numbers of granules around midbody, femoral pores, and circumorbital scales show relatively little variation compared with that seen among samples from the northeastern part of the range where four pattern types are found. Pattern Class E is regularly associated with high average numbers of dorsal granules and femoral pores and with type-III circumorbital scales.

Consistent correlations of color pattern and scutellation are not found among northeastern populations. Samples 1A and 2B have highly similar mean numbers of femoral pores ($P = 0.2$) and only type-I circumorbital scales, but differ significantly ($P << 0.001$) in dorsal granules. Samples 2B and 3C have identical mean numbers of both dorsal granules

and femoral pores but differ in circumorbitals. Within Class C there is a wide range of femoral pores and dorsal granules. The means of both these characters in sample 4C are much higher than in the other three samples of Class C, which are rather closely grouped. Samples 7D and 8D differ notably from one another in all three aspects of scutellation, but do not differ significantly from some samples of classes A, B, and C. Although sample 1A has a distinctly lower mean number of dorsal granules than any other population studied, this correlation of pattern and scutellation may not hold when adequate samples of Class A from other localities become available. For example, two specimens of Class A from Stone City, Pueblo County, Colorado, about 17 miles northwest of the site of sample 1A, have 82 and 87 granules around midbody. These counts bracket the mean of sample 2B, and 87 is two higher than the maximum recorded for sample 1A.

Perhaps the most striking feature of variation in *Cnemidophorus tesselatus* is the relative homogeneity of lizards of widespread Class E and the diversity of the populations occupying the minor remaining part of the geographic range.

SYMPATRIC CLONES

In an organism that reproduces parthenogenetically mutation may lead to the development of local populations composed of a variety of genetically different clones. There are a number of instances in which I suspect heterogeneity in local populations of *Cnemidophorus tesselatus*, but in which the relative contributions of genetic variation and phenotypic variation cannot be assessed. In two instances, however, there is good evidence of at least two clonal lines in one population.

Twenty-four specimens of *C. tesselatus* collected in the vicinity of Higbee, Otero County, Colorado, belong to pattern Class D and seven to Class C (samples 3C and 7D), which could merely be phenotypic variation within one clone, but there is a difference in the mean number of granules around midbody that correlates with color pattern. The mean of the Class C lizards is 86.1 ± 1.3 , that of Class D is 91.6 ± 0.6 ; the difference between the means is significant, $t = 4.178$, $P < < 0.001$ (see tables 1, 2, and 3). There is no significant difference in mean number of femoral pores, but two-thirds of the Class-C lizards have type-III circumorbital scales, whereas 70 per cent of the Class-D lizards have type I or II. Therefore, at least two clonal lines are represented at this locality; whether additional lines are present cannot be determined from the phenotypic evidence.

Lizards of pattern classes C and D also occur in the same local popula-

tions in San Miguel County, New Mexico, in the vicinity of Conchas Lake (samples 5C and 8D). Here the relative abundance of the two classes appears to be reversed, there being seven specimens of Class D and 21 of Class C. There is less difference between the classes in granules around midbody than in the Colorado example: Class-C mean, 88.7 ± 1.1 ; Class-D mean, 84.9 ± 1.1 ; $t = 1.945$, $P < 0.1$, > 0.05 . A similar degree of difference exists in the mean numbers of femoral pores: Class-C mean, 41.0 ± 0.5 ; Class-D mean, 38.9 ± 0.7 ; $t = 2.417$, $P = 0.02$. All seven Class-D lizards have type-III circumorbital scales, whereas the larger Class-C sample has 14 per cent each of types I and II and 71 per cent of type III.

The case for two clonal lines is less well supported than in the preceding example, and an additional factor must be considered. Sample 5C has a coefficient of variation of 5.46 per cent for granules around midbody, the largest of all 17 samples of *tesselatus* tabulated; the next highest is 4.60 per cent. The coefficient of variation for femoral pores is the second highest observed, 5.00 per cent, being exceeded only by the figure of 5.04 per cent for the sympatric sample 8D. Sample 5C (and possibly 8D as well) appears to be more variable than many other local samples, and a comparison of 5C with 8D may actually involve several clones rather than just two. Given an adequately large sample of lizards, one could test this supposition by plotting the numbers of femoral pores and granules around midbody on histograms and looking for the presence of curves with more than one mode, or by plotting on scatter diagrams and looking for clusters of spots. A more certain method of detecting obscure clones would be to utilize tissue transplantation. In this way, Kallman (1962b) demonstrated the existence of several clones in a local population of phenotypically identical gynogenetic fish, *Mollienesia formosa*.

COMPARISON OF VARIATION IN UNISEXUAL AND BISEXUAL FORMS

Cnemidophorus tigris is the principal bisexual species chosen for comparison with *C. tesselatus*. The two are referred to the same species group, and at one time were thought to represent only a single species (Burt, 1931). Their areas of distribution overlap broadly and, though there are differences in habitat selection, they can be found together in the same habitat.

Three samples represent *C. tigris* in the comparisons: one sample collected within an arc with a radius of 15 miles northwest to northeast of Lordsburg, Hidalgo County, New Mexico (*C. t. marmoratus*), and another collected 2 to 8 miles north of Portal, Cochise County, Arizona (*C. t.*

TABLE 4
VARIATION IN SCUTELLATION IN THREE SAMPLES OF *Cnemidophorus tigris*

Locality	Granules around Midbody					Femoral Pores				
	Mean $\pm \sigma_m$	Range	V%	N	Mean $\pm \sigma_m$	Range	V%	N		
Portal, Arizona	92.1 \pm 0.6	86–98	3.89	30	36.3 \pm 0.4	31–41	7.56	43		
Lordsburg, New Mexico	91.6 \pm 0.9	83–102	5.40	33	42.6 \pm 0.3	36–48	5.68	63		
Alamogordo, New Mexico	97.6 \pm 1.6	91–116	7.16	35	44.9 \pm 0.5	38–50	6.35	35		

gracilis) were utilized in a previous study (Zweifel, 1962); the third sample (*C. t. marmoratus*) is from the vicinity of Alamogordo, Otero County, New Mexico. The samples include both male and female lizards. It might have been better to use only female *tigris* in the comparisons, but the use of both sexes provided samples of adequate size without drawing the sample from too large an area. The use of bisexual samples is defensible on the ground that no sexual dimorphism in scutellation is evident. For example, in the Alamogordo series of 13 females and 22 males, the value of *t* for the mean number of femoral pores is 1.003 and for granules around midbody is 0.922. The probability that the means of male and female samples are the same is 0.3 or higher.

The great variation of color pattern in *tesselatus* is not unusual for *Cnemidophorus*. There are widespread bisexual species with as much or more variation, *tigris*, *costatus*, and *septemvittatus*, for example, and others such as *sexlineatus* that are less variable. There are analogous patterns in *tesselatus* and *tigris*. The striped and spotted pattern of Class A is similar to that of some populations of *C. tigris aethiops* of Sonora; Class C is nearly duplicated in *C. tigris stejnegeri* of southern California (I reject the synonymization of this form with *C. t. multiscutatus* of Baja California; see Burger, 1950; and Zweifel, 1958); some individuals of *C. tigris marmoratus* closely resemble strongly cross-barred *tesselatus* of Class E and others with a finer pattern resemble Class F.

Cnemidophorus tesselatus does not differ from bisexual species in the extent of variation in granules around midbody. The range among 511 specimens of *tesselatus* is from 75 to 112 GAB. Comparable ranges for bisexual species are (Zweifel, 1959; Duellman and Zweifel, 1962; Beargie and McCoy, 1964; and unpublished data): *costatus*, 91–121 (*N* = 522); *tigris*, 83–116 (*N* = 135); *angusticeps*, 90–143 (*N* = 232); and *septemvittatus*, 69–110 (*N* = 129). The variation of local populations, however, presents a strikingly different picture, for there are marked differences between *tesselatus* and *tigris* in range of variation and in dispersion in local populations.

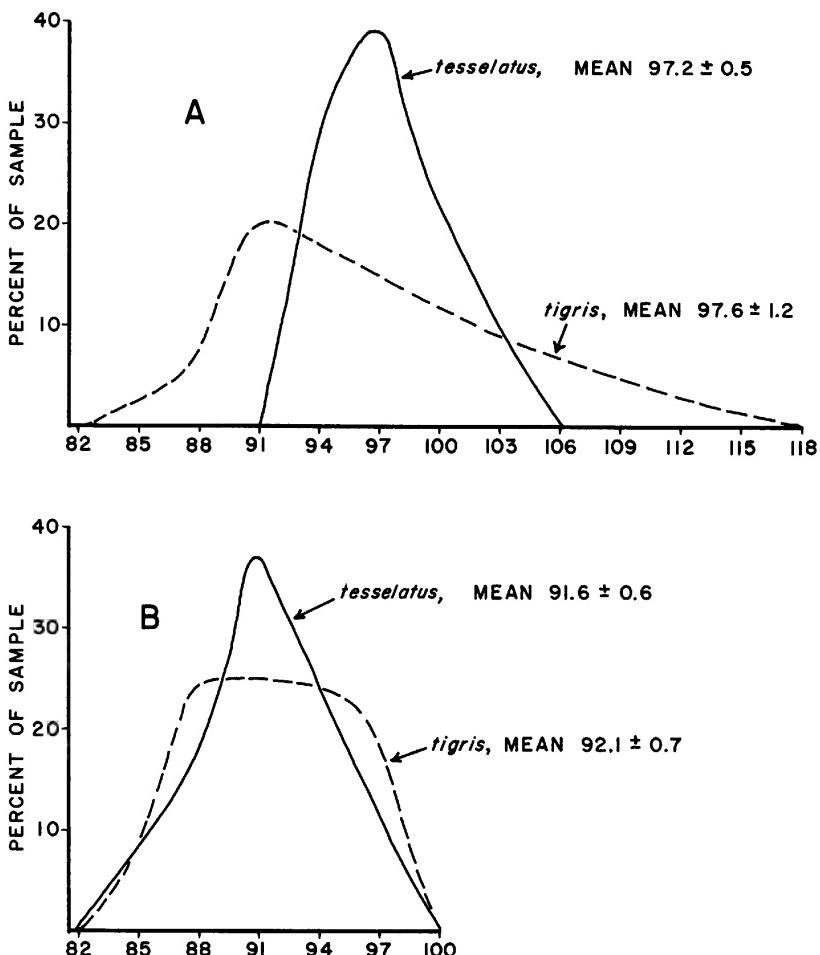


FIG. 7. Frequency distribution of granules around midbody in *Cnemidophorus tigris* and *C. tesselatus*. A. *Tigris*, Alamogordo, Otero County, New Mexico, and *tesselatus*, sample 11E, Culberson County, Texas. B. *Tigris*, vicinity of Portal, Cochise County, Arizona, and *tesselatus*, sample 7D, Otero County, Colorado. See table 8 for raw data.

Differences in dispersion are evident when coefficients of variation (V) are compared (tables 1 and 4). Among 17 samples of *tesselatus* the value of V exceeds 4.0 per cent only three times, the highest value being 5.46 per cent, whereas in the samples of *tigris*, V equals 3.89, 5.40, and 7.16 per cent. Differences in dispersion are shown in figure 7 and table 8. The samples compared have similar sizes, virtually identical means, and are

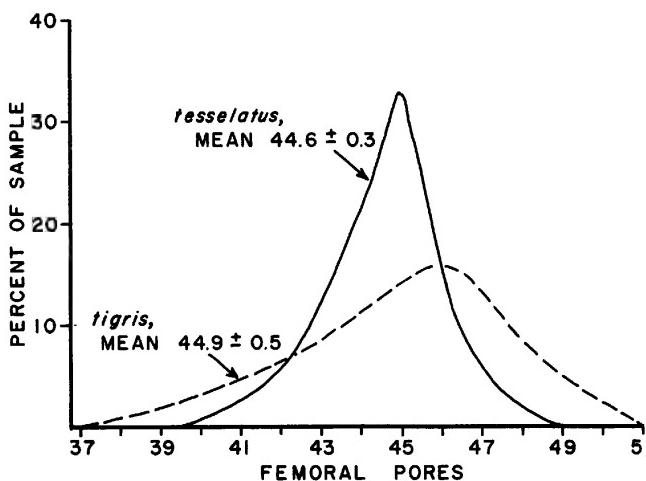


FIG. 8. Frequency distribution of femoral pores in *Cnemidophorus tigris* from Alamogordo, Otero County, New Mexico, and *C. tesselatus* from Sierra County, New Mexico. See table 8 for raw data.

from restricted areas. The difference in dispersion is most striking in figure 7A, but even the relatively invariable sample of *tigris* from Portal (fig. 7B) has a flatter distribution curve than its counterpart. A comparison of the coefficients of variation for *tigris* with those of samples of other bisexual species (table 9) shows that the values for *tigris* are not abnormally high.

Another means of analyzing variation is to compare the variances of pairs of samples by F tests. The results of F tests among nine samples of *tesselatus* are given in table 5. In 21 of 36 pairs the probability that the variances are the same is 0.2 or greater, and in only seven pairs does the probability reach 0.02 or less. This fact suggests that distribution about the mean is similar from sample to sample. A similar though not so extreme situation prevails among the three populations of *C. tigris*: one pair has a low level of probability, <0.01, whereas the others are 0.1 or 0.2 (table 6).

Dissimilarity of variances of *tesselatus* and *tigris* is made evident by the F test (table 7). Among 27 interspecific pairs, there are 13 with a probability of 0.02 or less and 10 in which P is equal to or greater than 0.20.

The range in number of femoral pores in the whole sample of *tesselatus*, 36–48 ($N = 517$), is more restricted than that in large samples of bisexual species (Zweifel, 1959; Duellman and Zweifel, 1962; Beargie and McCoy, 1964; and unpublished data): *costatus*, 29–49 ($N = 527$);

TABLE 5
COMPARISON OF THE VARIANCES OF THE GRANULES AROUND MIDBODY AMONG NINE SAMPLES OF *Cnemidophorus tessellatus* BY MEANS OF F TESTS
(Figures given are the value of F and the probability that the variances compared are the same.)

Sample ^a	2B	4C	7D	11E	12E	15E	16E	17E
1A	2.49 (0.05)	1.07 (>0.20)	1.34 (>0.20)	1.20 (>0.20)	1.92 (>0.10)	1.57 (>0.20)	2.75 (>0.02)	3.14 (0.01)
2B	—	2.67 (0.02)	1.86 (0.20)	2.07 (0.05)	1.28 (>0.20)	1.59 (0.20)	1.10 (>0.20)	1.26 (>0.20)
4C	—	—	1.43 (>0.20)	1.28 (>0.20)	2.06 (0.10)	1.67 (>0.20)	2.91 (>0.01)	3.35 (<0.01)
7D	—	—	—	1.11 (>0.20)	1.44 (>0.20)	1.17 (>0.20)	2.05 (0.10)	2.34 (0.05)
11E	—	—	—	—	1.60 (0.20)	1.30 (>0.20)	2.28 (>0.02)	2.61 (0.02)
12E	—	—	—	—	—	1.23 (>0.20)	1.43 (>0.20)	1.63 (0.20)
15E	—	—	—	—	—	—	1.75 (0.10)	2.00 (>0.20)
16E	—	—	—	—	—	—	—	1.14 (>0.20)

^a See figure 3 for localities and table 1 for sizes of samples.

TABLE 6
COMPARISON OF THE VARIANCES OF THE GRANULES AROUND MIDBODY AND FEMORAL PORES AMONG THREE SAMPLES OF *Cnemidophorus tigris*
BY MEANS OF F TESTS
(Figures given are the value of F and the probability that the variances of the samples are the same.)

Sample ^a	Granules Around Midbody Lordsburg, New Mexico	Femoral Pores Lordsburg, Arizona	Granules Around Midbody Lordsburg, Arizona	Femoral Pores Lordsburg, New Mexico	Femoral Pores Portal, Arizona
Alamogordo, New Mexico	1.99 (<0.10)	—	3.79 (<0.01)	1.39 (>0.20)	1.08 (>0.20)
Lordsburg, New Mexico	—	1.90 (0.10)	—	—	1.28 (>0.20)

^a See table 3 for other statistical data.

TABLE 7

COMPARISON OF THE VARIANCES OF THE GRANULES AROUND MIDBODY AND OF THE FEMORAL PORES AMONG NINE SAMPLES OF *Cnemidophorus tesselatus* AND THREE OF *Cnemidophorus tigris* BY MEANS OF F TESTS
 (Figures given are the value of F and the probability that the variances of the samples are the same.)

Sample ^a of <i>tesselatus</i>	Alamogordo, New Mexico	<i>tigris</i> Lordsburg, New Mexico	Portal, Arizona
Femoral pores			
1A	4.30 (<0.01)	3.09 (<0.01)	3.98 (<0.01)
2B	3.33 (<0.01)	2.40 (<0.05)	3.08 (<0.01)
4C	3.69 (<0.01)	2.66 (0.02)	3.42 (<0.01)
7D	2.89 (0.01)	2.08 (0.05)	2.68 (0.01)
11E	4.56 (<0.01)	3.29 (<0.01)	4.22 (<0.01)
12E	2.81 (<0.01)	2.02 (0.05)	2.60 (<0.01)
15E	3.58 (<0.01)	2.58 (<0.01)	3.31 (<0.01)
16E	3.51 (<0.01)	2.53 (<0.01)	3.25 (<0.01)
17F	2.63 (<0.05)	1.89 (0.10)	2.43 (<0.05)
Granules around midbody			
1A	7.51 (<0.01)	3.78 (<0.01)	1.98 (0.10)
2B	3.02 (<0.01)	1.52 (0.20)	1.25 (>0.20)
4C	8.03 (<0.01)	4.04 (<0.01)	2.12 (0.05)
7D	5.61 (<0.01)	2.82 (0.02)	1.48 (>0.20)
11E	6.25 (<0.01)	3.14 (<0.01)	1.65 (0.20)
12E	3.91 (<0.01)	1.96 (0.02)	1.03 (>0.20)
15E	4.80 (<0.01)	2.29 (<0.05)	1.27 (>0.20)
16E	2.74 (<0.01)	1.38 (>0.20)	1.38 (>0.20)
17F	2.39 (<0.05)	1.20 (>0.20)	1.58 (>0.20)

^a See figure 3, table 1, and table 3 for localities and other statistical data.

tigris, 31–50 ($N = 193$); *angusticeps*, 31–49 ($N = 232$); *septemvittatus*, 30–45 ($N = 161$).

The coefficient of variation in femoral pores is low for the 17 samples of *tesselatus* tabulated (table 1), exceeding 4.00 per cent only five times, with a maximum of 5.04 per cent. In contrast, V is higher in *tigris*: 5.68, 6.35, and 7.56 per cent (table 4). Again, values for samples of other bisexual species are high (table 9). An example of the difference in distributions is illustrated in figure 8 and table 8.

TABLE 8
 NUMBERS OF GRANULES AROUND MIDBODY (MIDPOINTS OF GROUPS OF THREE) AND OF FEMORAL PORES IN
 SAMPLES OF *Cnemidophorus tesselatus* AND OF *Cnemidophorus tigris*
 (These data are shown as percentages in figures 7 and 8.)

Sample ^a	<i>N</i>	Mean	Granules Around Midbody								
			85	88	91	94	97	100	103	106	109
<i>tesselatus</i> , 11E, <i>tigris</i> , Alamogordo, New Mexico	33	97.2 ± 0.5	—	—	10	13	7	3	—	—	—
<i>tesselatus</i> , 7D, <i>tigris</i> , Portal, Arizona	35	97.6 ± 1.6	1	1	8	7	4	5	3	1	2
	24	91.6 ± 0.6	2	4	9	6	3	—	—	—	—
<i>tesselatus</i> , 13E, <i>tigris</i> , Alamogordo, New Mexico	30	92.1 ± 0.6	1	8	7	7	—	—	—	—	—
	38	39	40	41	42	43	44	45	46	47	48
	—	—	—	—	2	5	7	12	6	1	2
	36	44.6 ± 0.3	—	1	—	—	—	—	—	—	—
	35	44.9 ± 0.5	1	1	1	1	4	2	4	6	5
										4	1
											1

^a See figure 3 for *tesselatus* localities.

Comparison of variances among nine samples of *tesselatus* by means of F tests indicates that the distributions are highly similar in all. In only two of 36 pairs is the value of P less than 0.2, and in these instances it is greater than 0.1. The situation among the three samples of *tigris* is the same: all values of P are greater than 0.2. A comparison of samples of *tesselatus* with *tigris* reveals that, although each species is internally homogeneous, the species differ notably. Among 27 pairs of *tigris* and *tesselatus*, P is 0.01 or less in 20 and 0.05 or less in 26 (table 7).

Cnemidophorus tesselatus shows ranges of variation in pattern and scutellation quite similar to those of widely distributed bisexual species of *Cnemidophorus*.

TABLE 9

COEFFICIENTS OF VARIATION FOR FEMORAL PORES AND GRANULES AROUND MIDBODY
IN SEVERAL POPULATIONS OF *Cnemidophorus*

Species	Locality	Femoral Pores		Granules around Midbody	
		V%	N	V%	N
<i>C. angusticeps angusticeps</i>	Piste, Yucatan	5.98	(78)	7.88	(78)
<i>C. communis communis</i>	Colima, Colima	6.84	(34)	5.35	(34)
<i>C. costatus barrancorum</i>	Guirocoba, Sonora	7.42	(22)	6.43	(21)
<i>C. costatus griseocephalus</i>	Alamos, Sonora	6.04	(24)	6.33	(24)
<i>C. costatus huico</i>	San Blas, Nayarit	3.12	(35)	6.66	(35)

dophorus. When samples from restricted areas are compared, however, *tesselatus* usually exhibits much less variation than the bisexual form, *C. tigris*. Such is true of color pattern, though not readily demonstrated objectively, and can be shown statistically in the case of scutellation. In *tesselatus* the grouping about the mean is tighter than in *tigris* and the curve less skewed (figs. 7 and 8). Presumably the differences in variation of local populations are a consequence of the modes of reproduction. Recombination in *tigris* results in local populations that are genetically and phenotypically more diverse than is the case in parthenogenetic *tesselatus*.

THE PATTERN OF EVOLUTION IN *CNEMIDOPHORUS TESSELATUS*

SOURCES OF VARIATION: Inherent to the bisexual mode of reproduction is a store of genetic variability that is largely hidden in the form of recessive genes. Bisexual reproduction with resultant recombination produces offspring with a variety of new genotypes. This genotypic diversity

is presumably of great importance in permitting populations to adapt to new or changing environments—in short, to evolve. A parthenogenetic species, however, cannot produce genetically different individuals by combining the gametes of parents who are certain to have different genetic constitutions. One might suppose that a parthenogenetic species would be an evolutionary dead end, perhaps able to flourish under conditions in which it was particularly well adapted, but with little potential for increasing its range of variation and adaptability. *Cnemidophorus tesselatus* refutes this supposition by demonstrating ranges of variation (in presumably genetically determined characters) that are quite similar to those of bisexual species.

The mechanism of parthenogenesis in *tesselatus* remains to be ascertained. Some fishes (Kallman, 1962a) and salamanders (MacGregor and Uzzell, 1964) are gynogenetic: foreign sperm provides the stimulus for embryonic development but contributes no genetic material. Probably such is not true of *Cnemidophorus*, for populations consisting only of females live where there are no bisexual species. I am uncertain whether this fact is true of *C. tesselatus*, though the situation may occur locally. Commonly, two parthenogenetic species are sympatric with one bisexual form. In one small area in western New Mexico three unisexual species occur in the same habitat with one bisexual species.

Parthenogenetic reproduction may operate in a variety of ways. In generative or haploid parthenogenesis, chromosome reduction occurs and the unfertilized egg develops as a haploid individual. Somatic parthenogenesis producing diploid individuals may be of two kinds: (1) automictic, in which the usual two meiotic divisions take place and the diploid chromosome number is restored through the fusion of the haploid nuclei thus produced, and (2) apomictic, in which "neither chromosome reduction nor fusion of nuclei nor any corresponding phenomenon" occurs in the eggs developing parthenogenetically (Suomalainen, 1950, p. 197).

Darevsky and Kulikova (1961, p. 172) reported that in parthenogenetic *Lacerta saxicola armeniaca* the first and second meiotic divisions take place normally. Parthenogenesis is thus automictic in the sense of Suomalainen, who made the following pertinent statement (1950, p. 222): "It must be noticed that in the most common automictic types of parthenogenesis . . . heterozygosity either obligatorily . . . or at least often . . . is replaced by homozygosity. This implies that if a gene mutation occurs in such an animal the changed gene usually soon becomes homozygous. In this way species with automictic parthenogenesis sooner or later will become split into a number of distinct races." Furthermore (p. 221), "a heterozygous female . . . may in regard to at least a number of genes give rise both to

homozygous and heterozygous offspring." As yet there is no cytological evidence for the nature of parthenogenesis in *Cnemidophorus*, but the great geographic variation seen in *C. tesselatus* suggests that the mechanism may be automictic.

In an automictic situation, a recessive mutation may become homozygous and thus may be exposed to selection in the first generation or soon thereafter. Thus, any mutation is likely to be exposed to selection quite quickly. If it is of high selective value, rapid evolution may result. A recessive mutation occurring in a bisexual species is much less likely to be exposed to selection so quickly, for its phenotypic expression depends on the mating of individuals bearing the same allele. The allele may, however, be retained in the gene pool even if not of positive selective value at the moment, whereas in the parthenogenetic species the mutant gene may more readily be lost.

The possibility that mating and normal fertilization occasionally take place must be considered. Males of *tesselatus* are excessively rare, but if a male were fertile and were capable of fertilizing eggs that otherwise would have developed parthenogenetically, even this rare event could contribute significantly to the variation of the species. If *tesselatus* behaves like *Lacerta siccicola*, however, there is little possibility that successful bisexual breeding occurs. Darevsky and Kulikova (1964) reported that hybridization between bisexual and parthenogenetic "races" of *Lacerta siccicola* produces triploid females that invariably are sterile.

Interspecific hybridization is another possibility. Populations of *Cnemidophorus tesselatus* often are sympatric with those of one or more bisexual species, and the chance of interspecific mating must occur much more frequently than that of intraspecific mating. If fertile interspecific mating occurs, however, it must be decidedly uncommon, judged from the scarcity of individuals peculiar enough to have resulted from such a union.

I have found only one specimen of *C. tesselatus* that differs strikingly from all others with which it is associated geographically. This lizard, U.N.M. No. 3125, from 1 mile west of Socorro, Socorro County, New Mexico, is a female of large adult size (S-V 94 mm.) with tiny gonads. The lizard has only 75 granules around midbody, compared to a mean of 95.5 (89–105) for 42 other individuals of *tesselatus* from the vicinity of Socorro. The minimum number of granules otherwise recorded for the species is 76 in sample 1A from Pueblo County, Colorado. Other scale characters are normal for lizards from Socorro. The specimen is also peculiar in color pattern: it has irregular paravertebral and upper lateral lines, and the vertebral and upper lateral dark fields are invaded by light areas from both sides, but the continuity of the dark fields is broken only in-

frequently. Instead of the dark and light lateral bars or dark quadrangles of other lizards of the Socorro area, this individual has large, irregular light spots with dark borders that more or less suggest the vertical bars.

Unfortunately, there are no other specimens of *tesselatus* from the exact locality where U.N.M. No. 3125 was taken, so it is unknown whether this individual is unique or typical of an established clone. Darevsky and Kulikova (1964) reported that the gonads of the triploid females of *Lacerta saxicola* resulting from the breeding of normal males with parthenogenetic females were poorly developed. The presence of tiny gonads in a specimen of adult size suggests that U.N.M. No. 3125 may in fact be of hybrid origin. *Cnemidophorus tigris* and *C. inornatus* are the bisexual species present in the area. The low number of granules in U.N.M. No. 3125 might favor *inornatus* over *tigris* as the possible male parent. However, no matter whether its peculiarities are due to gene mutation, hybridization, or ploidy, U.N.M. No. 3125 offers dramatic evidence of the markedly divergent individuals that an otherwise conservative population can produce.

ADAPTIVE SIGNIFICANCE OF VARIATION: Virtually all but the most highly restricted populations of vertebrates show geographic variation, but in relatively few instances is the adaptive significance of the variation as clear as it is, for example, in the embryonic temperature tolerance of *Rana* (Moore, 1949), or in the background color matching of lizards (Norris and Lowe, 1964). Variation in *tesselatus* has two major facets: the relative uniformity throughout the area occupied by Class E compared with the variation seen in the rest of the range, and the small amount of variation seen in local populations everywhere.

Catastrophic selection may play a part. The conspicuously variant populations of *Cnemidophorus tessellatus*, notably those in Colorado (1A, 2B, 3C, 4C, and 7D) and southwestern New Mexico (17F), are situated at the margin of the range. Populations in these areas are likely to be small and quite restricted geographically, as I have noted in New Mexico and as Maslin (*in litt.*) observes in Colorado. Catastrophic selection such as H. Lewis (1962, p. 270) described could be an important factor in the survival and variation of such marginal populations: "Catastrophic selection, whereby an entire population is suddenly eliminated by an environmental extreme except for one or more exceptionally adapted individuals, provides the conditions necessary for the establishment of a population characterized by deviant genomes. By elimination of the parental population, catastrophic selection isolates the survivors and their progenies in an open habitat to which they are adapted."

In addition to permitting the differential survival of exceptionally well-adapted individuals, catastrophic action of an environmental extreme

might lead to chance survival of one of two or more genomes of similar adaptive value. For example, where distinct clones exist sympatrically the relative numbers of individuals of different clonal types may fluctuate owing to chance survival during periods of environmental stress. Replacement of one clone by another, such as may have occurred in at least one locality (see the following section on Taxonomy), could result purely by chance if the population size were reduced enough. A parthenogenetic population, with its higher reproductive potential, should better be able than a bisexual one to withstand drastic reduction in numbers and should be able to recover faster.

It might be thought peculiar that local populations of *tesselatus* are not more variable, since one might expect numerous clonal lines to be established. Two possible explanations for the striking uniformity seen in local populations are: (1) selection greatly favors the best-adapted clone, and mutants are unable to establish competing clones; (2) the mutation rate is so low that competing clones rarely are initiated. There seems to be no firm basis for deciding if either of these explanations is correct, though the sympatric existence of pairs of clones in at least two regions indicates that at least in these places selection is not sufficiently rigid to prevent two different genetic lines from coexisting. Using the sensitive technique of tissue transplantation, Kallman (1962b) found that individuals of the parthenogenetic fish *Mollienesia formosa*, belonging to only two clones, made up 80 per cent of a local population and a third clone made up another 10 per cent. Perhaps a long-term field study would show that the relative numbers of members of a clonal pair varies in time and space in response to changing conditions.

ADVANTAGES AND DISADVANTAGES OF PARTHENOGENETIC REPRODUCTION: A consideration of how few species of vertebrates are parthenogenetic leads to the conclusion that this mode of reproduction is either generally unfavorable or, if favorable, unattainable. The presence of six or more apparently parthenogenetic species among about 30 to 40 comprising the genus *Cnemidophorus* suggests that at least in some circumstances parthenogenesis may be of considerable selective value.

The outstanding feature of a parthenogenetic population from the viewpoint of population ecology is that all adult members have the potential of contributing young to the following generation. If fecundity, age at maturation, and population age structure are similar in two species, a parthenogenetic population could produce twice as many young in a breeding season as a comparable bisexual population. The geometric rate of increase could lead in a few generations to a vast preponderance of the parthenogenetic form.

Milstead (1957, table 2) gave data on the relative numbers of *Cnemidophorus* of six species with overlapping distributions. He recorded the number of specimens obtained in each of several habitats at four localities in west Texas. At three of these localities one or two unisexual forms occur. Three species present in the Sierra Vieja are *Cnemidophorus inornatus* (*C. perplexus* of Milstead), *C. exsanguis* (*C. sacki* of Milstead), and *C. tesselatus*. The first of these is a small, bisexual species; the other two are all-female and of similar size, larger than *C. inornatus*. In plains habitats, *inornatus* (312 specimens) greatly outnumbered *exsanguis* (15) and *tesselatus* (55), though in one specific habitat within the plains, Creosote Bush-Catclaw-Blackbrush, the numbers of *inornatus* (42) and *tesselatus* (34) were more nearly equal. In roughland habitats *inornatus* was absent and *exsanguis* outnumbered *tesselatus* 130 to 14.

At La Mota Mountain *C. tesselatus* and the bisexual *C. tigris* were the dominant species. All 104 specimens of *tigris* and 94 of 98 *tesselatus* came from four plant associations. In three associations *tigris* dominated by about six to four, whereas in the fourth the ratio was approximately seven to three in favor of *tesselatus*.

On the Stockton Plateau *C. tesselatus* and the bisexual *C. gularis* (*C. sacki* of Milstead) were the common species and occurred in approximately equal numbers. Where both species were present one was strongly dominant, outnumbering the other by a minimum of 2.2 to 1. In one association *gularis* was exclusive and in another strongly dominant, whereas in two associations *tesselatus* was virtually exclusive.

Milstead's data indicate that parthenogenetic populations are not necessarily denser than those of congeneric bisexual species with which they are sympatric. Obviously, reproductive potential is only one of an assortment of factors influencing habitat distribution and determining the outcome of competitive interactions.

The effect of parthenogenesis from the viewpoint of population genetics is similarly ambiguous. A parthenogenetic population consisting of one or a few similar clones that were particularly well adapted to the existing conditions might have an advantage over a bisexual population that, in effect, sacrificed some of its offspring in more frequent deleterious gene recombination. But if the parthenogenetic form could not respond quickly enough by genetic adaptation to changing conditions, the population might be at a disadvantage compared with a bisexual one able more readily to draw upon stored genetic variability.

The success of a parthenogenetic population may depend on the achievement of a mutation rate well suited to the particular local situation. Under unusually static environmental conditions, an already well-

adapted population might prosper with an extremely low mutation rate because the majority of mutations are ill adaptive or non-adaptive. With more variable conditions, however, the rate probably would be sufficiently high to provide material for an adaptive response to changing conditions but not so high as to dilute the population with ill-adapted individuals and thus significantly lower the general level of adaptedness. The ideal mutation rate might closely resemble the rate at which recessive mutations become homozygous in a comparable bisexual population. With its greater reproductive potential, however, a parthenogenetic population should be able to afford the higher loss accompanying a higher rate.

A genotype that permitted an individual to live under a wide variety of habitat conditions could compensate for a low potential for genetic change on the population level. But lizards of the genus *Cnemidophorus* do not in general show a wide ecological valence. Though *tesselatus* occupies a variety of habitats, in any one region the populations appear to be highly restricted. The reasons for habitat restriction are not at all clear. Milstead (1957) concluded that interspecific competition is the most important factor responsible for ecological separation among several species of *Cnemidophorus*, and that competition is avoided by the choice of different habitats or different areas. However, his conclusions may require review now that it is known that he was dealing with six species rather than four as he thought.

RELATIONSHIPS AMONG GEOGRAPHIC POPULATIONS: The color-pattern classes represent a graded series with respect to complexity of pattern. Four of the pattern types, A, B, C, and E, are essentially a linear series, while types D and F may represent offshoots of C and E, respectively. Pattern type A, with its persistent stripes and field spots, shows little ontogenetic change and may be the most primitive pattern. Change from A to B, B to C, and C to E takes place in relatively small steps, but the end product is quite different from the presumably primitive type A.

It is of more than casual interest that the four "main line" pattern types not only make a logical morphological series, but also have a corresponding geographic arrangement (fig. 1): Class A is confined to a few localities at the northernmost edge of the range of the species, while B, C, and E progress in allopatric steps to the south. From this arrangement, one might infer that successive genetic changes accompanied (or permitted) the southward spread of the species from the northern area occupied by the presumably primitive pattern type. Pattern Class D may have been produced twice as a sympatric derivative of Class C, and Class F may represent a far-western isolate derived from Class E.

This seemingly logical arrangement is not easy to reconcile with the

climatic history of the region. Probably as recently as 5000 to 10,000 years ago much of the area now occupied by *Cnemidophorus tesselatus* had a cooler and moister climate. Much of the present range, the northern part in particular, could not have harbored the species, which must have invaded at least the northern area since the terminal phase of the Wisconsin glaciation. If dispersal has been from south to north, the primitive form, which was the first to move north, may now exist only as a peripheral relict, having been replaced by more highly evolved types over the rest of the range. Similar reasoning may be used to explain the present distribution of types B and C, with the most recently evolved major type, E, occupying the greatest area. Climatic fluctuations even in postglacial time may have influenced populations profoundly, particularly at the periphery of the range, and there is evidence of a replacement of pattern types (and, hence, clones) at Pueblo, Colorado (see the following section on Taxonomy). It is unlikely that the evolutionary and distributional history of *C. tesselatus* is as simple as the present distribution of pattern types seems to indicate.

Scutellation shows a less regular geographic arrangement than does color pattern. Although in general high mean numbers of body granules and femoral pores are characteristic of lizards of Class E, and lower averages characterize classes A, B and C, the clear replacement of one type by another that occurs in color pattern is not duplicated in scutellation.

INTERSPECIFIC RELATIONSHIPS: It has been customary to group *tesselatus* together with *tigris* and its relatives in the "tesselatus group," implying close phylogenetic relationship and common ancestry. I am, however, not convinced that *tesselatus* is most closely related to *tigris* or that the "tesselatus group" deserves distinction from the "sexlineatus group." Individuals of *tesselatus* may have color patterns similar to those seen in *tigris*, but the geographic and individual variation in *tesselatus* is such that with the choice of the appropriate population of *tesselatus* almost as strong a case could be made for close relationship to *C. septemvittatus*.

The nature of the mesoptychial scales deserves consideration: in *tigris* the scales along the anterior border of the mesoptychial fold are not strongly and abruptly differentiated from those within the fold, whereas in *tesselatus* as in species aligned with *sexlineatus* the scales along the anterior edge of the fold are notably enlarged. Other features of scutellation are either held in common by the species meriting comparison or are too variable to be of use.

There is no assurance that the populations I include in *Cnemidophorus tesselatus* represent a single line of descent. The several pattern classes could have arisen independently from one or more bisexual ancestors. This explanation seems to me to be unnecessarily complicated, especially

in the light of the graded nature of the geographical and morphological steps between pattern classes.

The relationships of *C. tesselatus* undoubtedly lie within the *tigris-sexlineatus* complex, but there is no certainty which species is ancestral, if indeed such an ancestor exists today.

TAXONOMY

TAXONOMIC CATEGORIES: The nomenclature of unisexual populations has not often been of immediate concern to students of reptiles or higher vertebrates. Darevsky (1962) referred unisexual and bisexual populations to the same species, *Lacerta saxicola*, though he observed that when hybridization occurs the offspring are sterile. The species concept here evidently is purely phenotypic, for not only did Darevsky and Kulikova (1964) recognize parthenogenetic subspecies of the bisexual *Lacerta saxicola*, but in one instance referred bisexual and parthenogenetic populations to the same subspecies. McCoy and Maslin (1962) discussed the problem of infraspecific nomenclature with particular reference to the unisexual species *Cnemidophorus cozumelus* and recognized two subspecies. These authors (1962, p. 626) made their position quite clear: "Our intent in using the subspecies category was to emphasize our opinion that we are dealing with two clonal complexes which, on the basis of morphological similarity, are more closely related to each other than they are to any other species of *Cnemidophorus*."

Lowe and Wright (1964) divided the unisexual form *Cnemidophorus exsanguis* into three species, describing two of them as new. Evidently there is considerable sympatry among these forms, in contrast to the situation in *C. cozumelus* and in the pattern classes of *C. tesselatus*. The differences between the species recognized by Lowe and Wright seem to be no greater than between the various pattern classes of *tesselatus*.

Cnemidophorus tesselatus is somewhat more complicated than *C. cozumelus* because of the greater amount of variation in all characters and because of the difficulty created by sympatric clones. Given only pairs of terminal populations such as 1A and 17F, or 1A and any Class-E population, I would not hesitate to regard them as different species. In these pairs there is no overlap in the important character of dorsal granules, the mean numbers of femoral pores are significantly different, and color patterns are grossly different. However, when annectant populations are considered, there are few places where clear-cut divisions can be made unless only a single character is considered. Short of recognizing each color-pattern type as a separate species, I see no reasonable alternative to grouping the populations in one species. Of course, the principal criterion of bi-

sexual species, the presence or absence of reproductive isolation, cannot be invoked here, but treating all the populations as one species emphasizes their presumed close relationship and common ancestry.

Several subspecies could be recognized if color pattern were given the main emphasis. By broadening the definition of Class C to include Class D, thus eliminating the problem of sympatric subspecies, one would have five readily diagnosed forms that replace one another geographically. I do not favor this solution because it submerges Class D (which itself may be diphyletic) and because of the great variation in scutellation present among the several samples of Class C. I think that the subspecies category has its greatest utility when used to denote populations differing in a number of characters that are well correlated geographically. Such is not the case with *C. tesselatus*, in which sample 4C has the color pattern of surrounding populations but scutellation much more like that of populations of the geographically remote Class E.

If subspecies were recognized, classes B, C, and F would require new names, whereas the name *Cnemidophorus grahami* Baird and Girard, 1852, would be available for pattern Class E. Baird and Girard (1852, p. 128) gave the locality for the two specimens on which the description of *C. grahami* was based as "between San Antonio and El Paso del Norte," Texas. Smith and Taylor (1950a, p. 188; 1950b, p. 362) restricted the type locality to Fort Davis, Jeff Davis County, Texas, but Cochran (1961, p. 98) noted that the entry in the catalogue of the United States National Museum (in contrast to the published locality) is merely "El Paso." An illustration of one of the cotypes (U.S.N.M. No. 3046b) shows an individual with the lateral bars typical of Class E (Baird, 1859, pl. 32, fig. 1). Smith and Burger (1949, p. 281) designated U.S.N.M. No. "3096a" (presumably a *lapsus* for 3046a) lectotype.

TYPE LOCALITY: Allocation of the name *Cnemidophorus tesselatus* to a particular population poses an unusual and perhaps unique problem. Smith and Burger (1949, pp. 277-278) restricted the type locality of *Cnemidophorus tesselatus* to Beaver Creek, Fremont County, Colorado. Basing his re-evaluation on the detailed itinerary accompanying the original description of *tesselatus* (Say, in James, 1823, pp. 50-51), Milstead (1953, pp. 411-413) showed that the type series more likely was collected at or close to Pueblo, Pueblo County, Colorado. Apparently unaware of Milstead's work, Maslin (1959, pp. 41-42) utilized more recently discovered information on the expedition on which the type series of *tesselatus* was collected in restricting the type locality to "the junction of Fountain Creek and the Arkansas River, Pueblo Co., Colorado." This agrees closely with Milstead's restriction, as the locality determined by Maslin is on the out-

skirts of Pueblo.

Lizards found in the vicinity of Pueblo at the present time are of pattern Class A; all 20 specimens from Pueblo are clearly of this class. The lizards described by Say in the original description just as clearly are not of this class: "The back and sides of the body and neck, are marked by nine or ten longitudinal lines, and eighteen or twenty transverse ones, dividing the whole surface in a tessellated manner, the interstitial quadrate spaces being black . . ." (Say, *in James*, 1823, p. 50). This description is not of the pattern class present at Pueblo today, which is characterized by six light lines (the interrupted vertebral line might be interpreted as a seventh) and dark fields that are marked with light spots or may be broken up into black quadrangles only in the lower lateral field. Only lizards of Class D qualify as 10-lined or, if the double vertebral is indistinctly paired, nine-lined. Also, the prominence given in Say's description to the tessellated pattern of the "whole surface" favors Class D (see fig. 2D).

Lizards of Class D have been collected closest to Pueblo in the vicinity of Higbee, Otero County, about 60 miles east and 40 miles south of Pueblo (70 miles straight-line distance). Lizards of Class B inhabit an intermediate area 23 to 26 miles southeast of Pueblo. In Colorado, *C. tesselatus* is quite local and spotty in its occurrence (T. Paul Maslin, *in litt.*), so it is possible that Class-D lizards remain to be discovered close to Pueblo. In any event, the rather precise information on the type locality and color pattern of *tesselatus* combines with the apparent absence today of that pattern class from the type locality to suggest that Class A has replaced Class D at this locality since the type series was collected (and later lost) in 1820.

The type series of *tesselatus* is not in existence, so the accuracy of Say's description cannot be checked. However, the differences between lizards of Class A and those described by Say make it certain that his specimens were not of Class A, and Class D is the closest fit. The problem, then, is: if one were to designate a neotype in order to fix the name *tesselatus* with one or the other pattern class, should one emphasize type locality or morphology? Two "qualifying conditions" for the designation of neotypes (Stoll, 1961, pp. 81, 83) are, in this instance, contradictory: (1) "evidence that the neotype is consistent with what is known of the original type-material, from its description and from other sources," and (2) "evidence that the neotype came as nearly as practicable from the original type-locality." My inclination would be to select a neotype from the Colorado population of Class D ("as nearly as practicable"), but, since I am not recognizing subspecies, there is no necessity to take the step, and I leave the matter in abeyance.

ORTHOGRAPHY: The name of the species as given in the original de-

scription is *Ameiva tessellata*. Burt (1931, p. 152) emended the name to *tessellatus* on the grounds that "the use of one 'l' constitutes a misspelling," and later (1933, pp. 246–247) reiterated this view. Similarly, Stejneger and Barbour (1943, p. 106) stated, "*C. tessellatus* by Say is *in errore* and should be *C. tessellatus*." Authors publishing since Burt have not been in agreement as to the proper spelling. The assumption that Say misspelled the specific name is not necessarily valid, for evidently both single and double "l" spellings are correct (Jaeger, 1944, p. 232). There seems to be no justification for emending the original spelling.

DIAGNOSIS: Because of the wide ranges of variation in pattern and scutellation, it is difficult to provide a brief diagnosis that will distinguish all *tessellatus* from all other *Cnemidophorus*. The following combination of characters is, with qualification, diagnostic: size moderate, maximum length from snout to vent about 100 mm.; three parietal, two frontoparietal, and four supraocular scales; mesoptychial scales enlarged, abruptly differentiated from granular scales in the mesoptychial fold; postantebrachial scales slightly enlarged.

The relationships of *C. tessellatus* probably lie with *Cnemidophorus tigris* (which along with its insular derivatives has been placed with *tessellatus* in the "tessellatus group") or with species in the *sexlineatus* group (Duellman and Zweifel, 1962). *Cnemidophorus tigris* is most easily distinguished from *tessellatus* by the nature of the mesoptychial scales: the mesoptychial fold of *tessellatus* is bordered by an enlarged row of scales that are markedly larger than the granular scales within the fold, whereas in *tigris* there are no conspicuously enlarged scales along the edge of the fold. *Cnemidophorus tigris marmoratus* and *C. tessellatus* may be confusingly similar in pattern, but the relative size of these scales is a reliable character for distinguishing the species.

Eight species in addition to *tigris* occur within the area inhabited by *Cnemidophorus tessellatus*. Three of these, *C. exsanguis*, *C. gularis*, and *C. septemvittatus* (*C. scalaris*), can be distinguished from *tessellatus* by their greater enlargement of the postantebrachial scales as well as by other characters. The degree of enlargement seen in *tessellatus* is equal to or less than that categorized by Duellman and Zweifel (1962, fig. 2B) as "slightly enlarged," whereas *exsanguis*, *gularis* and *septemvittatus* fit the "enlarged" category (*ibid.*, fig. 2C).

Cnemidophorus sexlineatus, *C. inornatus*, *C. uniparens* (see Wright and Lowe, 1965, p. 167, for the use of this name), and *C. velox* typically are smaller than *tessellatus* and have a striped pattern without spots or other marks in the dark fields. The maximum number of femoral pores is 35 in *sexlineatus* and 37 in *velox*, whereas the minimum in *tessellatus* is 36; thus,

this character will serve to distinguish the vast majority of *tesselatus*. The maximum number of body granules in *inornatus* is about 80, whereas all but the northernmost populations of *tesselatus* (out of the range of *inornatus*) have more than 80.

Cnemidophorus perplexus (= *C. neomexicanus* Lowe and Zweifel), the only species of the *sexlineatus* group with granular postanteriorbrachials, is readily distinguished from *tesselatus* by the number of body granules. The maximum GAB in *perplexus* is 80, whereas this low number normally occurs in *tesselatus* only in the northernmost populations in Colorado, well out of the area of sympatry with *perplexus*.

HABITAT AND DISTRIBUTION

HABITAT: The most complete information on the habitat of *Cnemidophorus tesselatus* was presented by Milstead (1957) who studied the ecological interrelationships of six species of *Cnemidophorus* (he regarded them as four species, one with three subspecies) in western Texas. He found *tesselatus* in a wide variety of plant associations in both plains and roughland habitats. In two of his study areas, Milstead found the greatest concentration of *tesselatus* in areas of rough topography, but in the third the lizards were most abundant in plains habitats, though roughland was present.

Frederick R. Gehlbach, who studied this species in the Guadalupe Mountains of New Mexico and Texas, states (*in litt.*) that *tesselatus* has a vertical range of from 3200 to 5500 feet, being most abundant from 3800 to 4600 feet. It is sympatric with *Cnemidophorus exsanguis*, *C. inornatus*, *C. gularis*, and *C. tigris*, and is one of the two most abundant lizards (the other is a *Holbrookia*) in "foothill uplands where there is a ground, half-shrub, and shrub stratum in juxtaposition."

In the Panhandle region of Texas, *tesselatus* occurs in rocky canyon habitats (Strecker, 1910). Lowe and Zweifel (1952) found *tesselatus* most abundant in a plains habitat, yucca-grassland association, in Socorro County, New Mexico, but recorded the species from other habitats as well. In desert regions *tesselatus* is present in riparian situations. Degenhardt (*in Minton, "1958"* [1959], p. 44), collecting beside the Rio Grande in Big Bend National Park, found these lizards "common along the river"; and Williams, Smith, and Chrapliwy (1960, p. 42) reported that "these lizards were collected along the Río Florida in a vegetation consisting of willows, cottonwoods and fairly heavy undergrowth."

While studying *Cnemidophorus tigris* (Zweifel, 1962), my assistants and I collected intensively in southeastern Arizona and adjacent New Mexico. We found *tesselatus* only along a 3-mile stretch of road through Ante-

lope Pass in the Peloncillo Mountains, Hidalgo County, New Mexico. The floor of the pass has an elevation of approximately 4300 to 4400 feet, and the low hills bordering the pass rise little more than 300 to 400 feet. Rocky hill slopes give way to a sandy intermittent stream course along the center of the pass. Shrubby vegetation, mesquite (*Prosopis*) and desert willow (*Chilopsis*) in particular, provides abundant shelter in the sandy areas, but the sparser and smaller bushes in areas away from the dry stream bed offer less protection.

Most specimens of *tesselatus* were taken in the sandy wash and in the more open areas of the pass, but one came from the creosote-bush (*Larrea divaricata*) association on the alluvial fan a mile outside (west) of the mouth of the pass. *Cnemidophorus tigris gracilis* is the predominant species of whiptail lizard in the creosote-bush association, but evidently it does not occur throughout the pass (as *tesselatus* does), being restricted to the western part (Zweifel, 1962, p. 757). *Cnemidophorus uniparens* is found throughout the region, being most common in grassy areas, but *Cnemidophorus exsanguis* is represented in our collections by only one individual from Antelope Pass. The latter species is commoner in more mesic situations, being most abundant in riparian oak woodland. Of the four species of *Cnemidophorus* that occur in this immediate area, three are presumably parthenogenetic.

Granite Gap, about 10 miles north of Antelope Pass, is a narrower break in the low mountains. The elevation is virtually the same, but the region is much rockier, with a more abrupt change from sandy and gravelly flats to bouldery uplands. Creosote bush and mesquite are shared with Antelope Pass, but ocotillo (*Fouqueria*) and several kinds of cactus also are prominent at Granite Gap. Although we collected more intensively here than at Antelope Pass, we did not find *Cnemidophorus tessellatus*. Both *C. tigris* and *C. uniparens* were common, but as at Antelope Pass we obtained only one *C. exsanguis*. The only other spot in western New Mexico where *tessellatus* has been taken is at an isolated basaltic hill in Animas Valley about 5 miles north of Animas, approximately 10 miles east-northeast of Antelope Pass. Charles M. Bogert took one *C. tessellatus* and one *C. tigris marmoratus* here in 1953.

DISTRIBUTION: The known distribution of *Cnemidophorus tessellatus* is mapped in figure 1. Because of the unpredictable choice of habitat of this species, it is difficult to judge how accurately the records reflect the true geographic range. The species does not occur in mountainous highlands and probably reaches its upper altitudinal limit at about 6000 feet. The western and northern edges of the range in New Mexico have been drawn with this fact in mind. Present information indicates that *tessellatus* penetrates south of the Rio Grande only along the Río Conchos, but it would be

astonishing if it were not found eventually in other areas in northern Chihuahua and Coahuila. The Rio Grande itself is not an absolute barrier to distribution, for not only is *tesselatus* present along the Río Conchos, but it is found also on the Mexican side of the river at Santa Elena Canyon, opposite Big Bend National Park.

In the Panhandle of Texas, *Cnemidophorus tessellatus* is associated with the canyon systems of the Canadian and Red River drainages, and the range may be interpreted as a tongue extending eastward from New Mexico. Tinkle (1959, p. 196) noted that *tesselatus* is not present in seemingly suitable habitat south of its region of known occurrence in the northern Panhandle.

The area between the Rio Grande Valley and western Hidalgo County, New Mexico, has not been well collected, and the apparent disjunction of the western population may merely reflect this lack of field work. It would be of particular interest to see to which pattern class intermediate populations conform, especially in view of the presence of Class E in southeastern Arizona.

SUMMARY

Cnemidophorus tessellatus is a species of lizard in which males are virtually absent. Hence, reproduction presumably is parthenogenetic. Variation of the species as a whole is similar to that of bisexual forms, but samples of local populations of *tesselatus* show greatly restricted variation in color pattern and scutellation in comparison to similar samples of the bisexual form *C. tigris*. Presumably this restriction results from the great reduction in recombination that is a consequence of unisexual reproduction. Five allopatric classes of color pattern are recognized in *tesselatus*. Populations of a sixth class occur in two widely separated areas, in each of which they are sympatric with another class. Differences in scutellation correlate with differences in color pattern of sympatric populations, indicating that two genetically distinct clonal lines coexist. The most widespread color-pattern class is relatively uniform in scutellation over a wide geographic area, whereas populations with more restricted geographic distributions tend to differ, in some cases markedly, from locality to locality. Differences in scutellation and color pattern among populations of *tesselatus* are similar to those that distinguish subspecies in bisexual species of *Cnemidophorus*. However, complications introduced by sympatric clones and discordant variation render the recognition of subspecies impractical in the unisexual species. Retention of all the populations within one species is recommended as best exemplifying their relationships, even though gene exchange between parthenogenetic populations manifestly is impossible.

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LOCALITY RECORDS AND SPECIMENS EXAMINED

The list below includes localities from which I have examined specimens and records from the literature. The following abbreviations are used:

- A.M.N.H., the American Museum of Natural History
A.N.S.P., Academy of Natural Sciences of Philadelphia
C.A.S., the California Academy of Sciences, San Francisco
C.U., Cornell University, Ithaca, New York
D.H.H., Donald H. Hahn, Alamosa, Colorado, private collection
J.W.W., field numbers of John W. Wright, specimens in the University of New Mexico Collection of Vertebrates, Albuquerque
K.U., University of Kansas Museum of Natural History, Lawrence
M.V.Z., Museum of Vertebrate Zoology, University of California, Berkeley
U.C.L.A., University of California, Los Angeles
U.C.M., University of Colorado Museum, Boulder
U.I.M.N.H., University of Illinois Museum of Natural History, Urbana
U.M.M.Z., University of Michigan Museum of Zoology, Ann Arbor
U.N.M., University of New Mexico Collection of Vertebrates, Albuquerque
W.G.D., field numbers of William G. Degenhardt, specimens in the University of New Mexico Collection of Vertebrates, Albuquerque

The letter following a specimen number or a series of numbers indicates the pattern class to which the specimen belongs.

UNITED STATES

ARIZONA: *Cochise County*: 22 miles southwest of Rodeo [Hidalgo County, New Mexico], U.C.M. Nos. 23312, 23314, E.

COLORADO: *Baca County*: Skull Creek, 4800 feet, U.C.M. No. 7166, C; 0.5 mile southeast of Carrizo Mountain, U.C.M. No. 7556, C; Cottonwood Creek, 15 miles south, 12 miles west, of Pritchett, U.C.M. Nos. 14813, 14814, 14816–14829, C; 27 miles south of Pritchett (Maslin, 1950, p. 91). *Fremont County*: Canon City, U.C.M. No. 3183, A. *Las Animas County*: Trinchera Canyon, 30 miles east-northeast of Trinidad, U.C.M. No. 10022, B; Chacuaca Creek, Mesa de Maya Ranch, U.C.M. No. 17857, C; 2 miles south of Potato Butte, Cottonwood Creek, Dodge Ranch, U.C.M. Nos. 7549–7555, 11261, C; Purgatoire River, 19 miles east of Model (Maslin, 1950, p. 90). *Otero County*: Higbee, U.C.M. No. 17336, A; 1 mile south of Higbee, U.C.M. Nos. 4956, D; 14835, 14838, 14849, 14852, 14854, 14860, C; 14830–14834, 14836, 14837, 14839–14848, 14850, 14851, 14853, 14855–14859, D; 2 miles south of Higbee, U.C.M. Nos. 14837, 14838, C; 14839–14841, D; 6 miles northeast of Higbee, U.C.M. No. 4955, D; 17 miles south of La Junta, U.C.M. No. 17334, D. *Pueblo County*: Vicinity of Pueblo, U.C.M. Nos. 10366–10374, 10376, 10377, 10379, 10381–10383, 10385, 10404, 14861–14863, A; Undercliff Station, 23 miles southeast of Pueblo, U.C.M. Nos. 14864–14882, B; mouth of Huerfano Canyon, 25 miles southeast of Pueblo, U.C.M. Nos. 16968–16972, 17333, A.M.N.H. No. 88205, B; foothills of Greenhorn Range, west of Pueblo (Maslin, 1950, p. 90); foothills near Rye and foothills east of Rye (Maslin, 1950, p. 90); near Stone City, D.H.H., 2 specimens.

NEW MEXICO: *Chaves County*: Cienega Macho, 24 miles northwest of Roswell, U.C.L.A. No. 4712, E. *De Baca County*: ½ mile west of Fort Sumner, M.V.Z. Nos. 49860–49863, E. *Dona Ana County*: 15 miles north of Las Cruces (Van Denburgh, 1924, p. 213); Texas Canyon, Organ Range (T. H. Lewis, 1950, p. 7); 8.4 miles west of Hatch, J.W.W. Nos. 1891, 2351–2357, E. *Eddy County (all Class E)*: Near Carlsbad, U.M.M.Z. No. 70076, U.N.M. No. 1175; 16 miles west of Carlsbad, near Cone Butte, U.N.M. No. 1176; 16 miles west, 5 miles north, of Carlsbad, U.N.M. No. 1177; Bat Cave Draw, Carlsbad Caverns, National Park Headquarters area, U.M.M.Z. Nos. 119535 [8 specimens], 121403 [2 specimens]; Rattlesnake Spring, ca. 7 miles southwest of White City, 3600 feet, U.M.M.Z. No. 119534 [6 specimens]; Oak Spring Canyon, 0.7 mile northwest of Carlsbad Caverns, National Park Headquarters, 3500 feet, U.M.M.Z. No. 121402 [2 specimens]. *Hidalgo County (all Class F)*: Antelope Pass, Peloncillo Mountains, 7–8 miles west of Animas, J.W.W. No. 1849, U.C.M. Nos. 14666–14668, A.M.N.H. Nos. 80681–80691, 84834–84836, 86994–86996; 10 miles west of Animas, A.M.N.H. No. 80680; 5 miles north of Animas, A.M.N.H. No. 73739. *Luna County*: 0.3 mile north of Nutt, J.W.W. No. 1582, E. *Otero County*: 7.5 miles (by road) east of La Luz Post Office, U.C.L.A. No. 4711, E; Tularosa (Smith and Burger, 1949, p. 281); Cornuda Mountains, U.M.M.Z. Nos. 71084 [2 specimens], 71085 [3 specimens], 71096, E; between Alamo Mountain and Cornuda Mountain, U.M.M.Z. No. 71086 [4 specimens], E. *Quay County (all Class C)*: 1 mile south of Logan, J.W.W. No. 815, A.M.N.H. No. 77450; 14.5 miles east of Tucumcari, K.U. Nos. 40269, 40270; Duke

Ranch, 4300 feet, 23 miles southeast of Tucumcari, M.V.Z. No. 72621. *Sandoval County* (all Class E): 5 miles west of San Ysidro, J.W.W. Nos. 517–521, 670, 671; 1½ miles south, ¾ miles west of San Ysidro, U.N.M. Nos. 6745, 6746; 7 miles south, 9 miles west, of San Ysidro, U.N.M. No. 6744; Jemez Creek, 2.1 miles north of Canyon, J.W.W. Nos. 534, 535; above Jemez Pueblo, U.N.M. No. 1171; Hagen, J.W.W. Nos. 637–639; 0.2 mile west, 0.1 mile north, of Hagen, J.W.W. Nos. 574, 575; 1.5 miles north, 1.3 miles west, of Hagen, J.W.W. Nos. 570–572; 2.4 miles south of Hagen, J.W.W. No. 640; ½ mile west of Placitas, J.W.W. Nos. 710–713, 731; 3.5 miles south, 1.5 miles east, of Warm Spring, J.W.W. No. 966. *San Miguel County*: Conchas Lake at south State Park Campground, J.W.W. Nos. 785–787, 793–797, 800, 801, 803, 804, C; 788, 798, 799, 802, 805, 822, D; 4 miles south, 11 miles east, of Conchas, J.W.W. Nos. 812–814, C; 811, D; 2 miles north of Variadero, J.W.W. Nos. 828–830, C; 5.5 miles south, 6.5 miles east of Variadero, J.W.W. No. 833, C; 1.5 miles west of Gate City, J.W.W. No. 834, C; 4.2 miles west of Gate City, J.W.W. No. 835, C. *Santa Fe County*: 23 miles south of Santa Fe, U.C.M. No. 7005, E. *Sierra County* (all Class E): 6.5 miles east, 1 mile north, of Engle, U.N.M. No. 3131; 7.4 miles west of Engle, J.W.W. Nos. 1393–1396; 0.7 mile west of Engle, J.W.W. Nos. 1397–1400; 0.5 mile west, 0.5 mile south, of Caballo, U.N.M. Nos. 3603–3605; 9 miles west of Caballo, K.U. No. 49579; 12 miles west of Caballo, K.U. Nos. 49580–49583; north end of Elephant Butte Dam, K.U. No. 12861; 25 miles west of Elephant Butte Dam, K.U. Nos. 13037, 13038; 1 mile east of Elephant Butte Dam, J.W.W. Nos. 1390, 1391; 7 miles east of Hillsboro, J.W.W. Nos. 1414–1417; Berrenda Creek, 3.2 miles north, 1.3 miles east, of Lake Valley, J.W.W. Nos. 1504–1512. *Socorro County* (all Class E): Casa Grande, 2 miles east of Lava, M.V.Z. No. 16411; 5 miles east of Escondido, U.N.M. Nos. 3106–3111; 3 miles south, 3 miles west, of Socorro, U.N.M. No. 3115; 1 mile west of Socorro, U.N.M. No. 3125; 1 mile north, 3 miles west, of Escondido, U.N.M. Nos. 3128–3130; 6.5 miles west, 2 miles south, of Socorro, U.N.M. Nos. 1177, 3601, 3602; 4 miles west, 3 miles south, of Socorro, U.N.M. Nos. 3606–3618; 5 miles east, 1 mile north of Socorro, J.W.W. Nos. 284, 285, 287; 3 miles north of Socorro, J.W.W. No. 443; 4.5 miles east, 1 mile north, of Socorro, U.N.M. No. 1178; 4.5 miles east, 2 miles north, of Socorro, U.N.M. No. 1179; 5 miles east, 1 mile north, of Socorro, U.N.M. Nos. 1180, 1181; Socorro, U.C.L.A. No. 3780; 7 miles west of Socorro, U.C.L.A. No. 3773, A.M.N.H. No. 92215; 9.7 miles west of Socorro, U.C.L.A. No. 3777; northeast base of Ladrone Mountains, U.N.M. No. 1172; 5.5 miles west, 3.3 miles south, of Socorro, J.W.W. Nos. 970, 971, 1052–1054; near San Marcial, K.U. Nos. 6731, 6732, A.M.N.H. No. 84833; between San Marcial and Elephant Butte Dam, K.U. Nos. 13031, 13032; 3.5 miles south, 7.5 miles east, of La Joya, U.N.M. No. 6748; 2.5 miles south, 7¾ miles east, of La Joya, U.N.M. No. 6747; 1 mile east of Tokay, J.W.W. No. 1341; 28 miles south-southwest of Bingham, U.C.L.A. Nos. 4713, 4714; 23 miles south-southwest of Bingham, A.M.N.H. No. 92216; 22 miles south-southwest of Bingham, A.M.N.H. No. 92214, U.C.L.A. No. 3771; 20 miles south-southwest of Bingham, A.M.N.H. No. 92213, U.C.L.A. Nos. 3757, 3758, 3760–3765, 3767–3769, 4715; 10 miles south-southwest of Bingham, U.C.L.A. No. 3776; 20.5 miles south of Bingham, A.M.N.H. No. 92217; 15 miles south of Bingham, U.C.L.A. No. 3779; Mockingbird Gap, Sierra Oscura, U.C.L.A. Nos. 3775, 4716, 4717; Springtime Canyon Road, 1.6 miles west of U. S. Highway 85, J.W.W. Nos. 1369–1376; Springtime Canyon Road, 3.3 miles west of U. S. Highway 85, J.W.W. Nos. 1364–1368. *Valencia County* (all Class E): 10 miles west of Las Lunas, U.N.M.

Nos. 1173, 1174; Correo, U.N.M. No. 1169; 1 mile west of Mesita, U.N.M. No. 6743; ½ mile north, 14 miles east, of Belen, U.N.M. No. 6749.

OKLAHOMA: *Cimarron County*: 5 miles east of Kenton (Blair, 1950, p. 234); 5 miles north of Kenton (Glass and Dundee, 1950, p. 30).

TEXAS: *Armstrong County*: Rush Creek, U.M.M.Z. No. 42320 [2 specimens], C, C.A.S. Nos. 33088–33090, C; Palo Duro Canyon, M.V.Z. No. 65803, C; 25 miles southwest of Claude (Tinkle, 1959, p. 196); 18 miles south of Claude (Brown, 1950, p. 124). *Brewster County*: Santa Elena Canyon, W.G.D. Nos. 998, 1263, 1264, E; 7 miles southwest of Santa Elena, C.U. No. 5131, E; 3 miles northeast of La-jitas, W.G.D. No. 1893, E; Tres Cuevas Mountains (Schmidt and Smith, 1944, p. 85); Chisos Mountains, Green Gulch, San Vicente, north of Burro Mesa (Brown 1950, p. 124). *Briscoe County*: 15 miles southeast of Silverton (Tinkle, 1959, p. 196); 12 to 17 miles northwest of Silverton (Fouquette and Lindsay, 1955, p. 410). *Culberson County*: 40 miles north of Van Horn, U.M.M.Z. No. 91495 [3 specimens], E; 20 miles east of Van Horn, U.C.M. Nos. 14433, 14435–14462, 14464–14469, E; 2 miles west of Van Horn, 16 miles southeast of Van Horn (Brown, 1950, p. 124); 35 miles west of Toyah, U.M.M.Z. No. 116705, E; 18 miles northwest of Kent, U.M.M.Z. No. 116706, E; 1 mile north-northwest of Pine Springs, 5.5 miles south-southwest of Pine Springs and Bear Canyon (F. Gehlbach, *in litt.*). *El Paso County*: El Paso, C.A.S. Nos. 39831–39833, E; Fort Bliss (Brown, 1950, p. 124). *Hudspeth County* (*all Class E*): 6 miles west of Sierra Blanca, M.V.Z. No. 52238; 8 miles west of Sierra Blanca, U.M.M.Z. No. 113122; 14.5 miles northwest of Allamore, U.I.M.N.H. Nos. 20010–20012. *Jeff Davis County*: Cherry Canyon, U.M.M.Z. Nos. 51702–51707, E; Phantom Lake, U.M.M.Z. No 51709, E; Davis Mountains, U.M.M.Z. No. 51710, E; Limpia Canyon, Madera Canyon (Brown, 1950, p. 124). *Potter County*: Potter County (no other data), U.M.M.Z. Nos. 69088–69092, C; 26 miles northwest of Amarillo, Palo Duro Canyon (Brown, 1950, p. 124). *Presidio County*: Porvenir (Smith and Burger, 1949, p. 281); 3 miles north of Porvenir, 12 miles east of Ruidosa, 10 miles west-southwest of Valentine (Brown, 1950, p. 124); La Mota Rancho, 63 miles south of Marfa (Milstead, 1953, p. 411); Sierra Vieja (Jameson and Flury, 1949, p. 64). *Randall County*: Randall County (no other data), U.M.M.Z. No. 69093 [2 specimens], C; 13 miles east of Canyon, U.C.M. Nos. 13550–13552, C; 12 miles southeast of Canyon (Tinkle, 1959, p. 196); 20 miles southeast of Amarillo (Fouquette and Lindsay, 1955, p. 410); Palo Duro Canyon (Brown, 1950, p. 124). *Reeves County*: Pecos Valley, U.M.M.Z. No. 51728, E; Weinacht's Draw, U.M.M.Z. Nos. 51711–51727, E. *Swisher County*: Tule Canyon, A.N.S.P. Nos. 12886, 12887, C. *Terrell County*: Stockton Plateau (Milstead, Mecham, and McClintock, 1950, p. 553). *Val Verde County*: Mouth of Pecos River (Brown, 1950, p. 124).

MEXICO

CHIHUAHUA (ALL CLASS E): Boca del Rio San Pedro, K.U. No. 51879; 1 mile east of La Cruz, U.I.M.N.H. Nos. 43746–43748; 4.6 miles north of La Cruz, U.I.M.N.H. No. 44652; 2–3 miles southwest of La Roquilla, U.I.M.N.H. Nos. 52222, 52223; Monteseco, U.I.M.N.H. No. 52225; Guardiola, U.I.M.N.H. Nos. 52226, 52227; between Piedras Negras and Manga, U.I.M.N.H. Nos. 52228–52230; Culebra, U.I.M.N.H. No. 52231; Boquilla Culebra, U.I.M.N.H. Nos. 52232–52234; Beneficio, U.I.M.N.H. Nos. 52235–52244; 2 miles north of Falomir, U.I.M.N.H. Nos. 52245–52249; 5 miles north of Falomir, U.I.M.N.H. Nos. 52250–

52255; 3 miles southwest of San Pedro, U.I.M.N.H. Nos. 52256-52264; 2-3 miles southwest of Cuchillo Parado, U.I.M.N.H. Nos. 52265-52279; El Fortin, U.I.M.N.H. No. 52280; near Alamos, U.I.M.N.H. Nos. 52281-52283; 2 miles north of Julimes, U.I.M.N.H. No. 52224.

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